RAPPORT L.NR. 6580-2013



ICP Waters Report 114/2013

Biodiversity in freshwaters: temporal trends and response to water chemistry



International Cooperative Programme on Assessment and Monitoring Effects of Air Pollution on Rivers and Lakes



Convention on Long-Range Transboundary Air Pollution

Norwegian Institute for Water Research

REPORT

- an institute in the Environmental Research Alliance of Norway

Main Office	Regional Office, Sørlandet	Regional Office, Østlandet	Regional Office, Vestlandet	Regional Office Central
Gaustadalléen 21 NO-0349 Oslo, Norway Phone (47) 22 18 51 00 Telefax (47) 22 18 52 00 Internet: www.niva.no	Jon Lilletuns vei 3 NO-4879 Grimstad, Norway Phone (47) 22 18 51 00 Telefax (47) 37 04 45 13	Sandvikaveien 59 NO-2312 Ottestad, Norway Phone (47) 22 18 51 00 Telefax (47) 62 57 66 53	Thormøhlens gate 53 D NO-5006 Bergen Norway Phone (47) 22 18 51 00 Telefax (47) 55 31 22 14	Pirsenteret, Havnegata 9 P.O.Box 1266 NO-7462 Trondheim Phone (47) 22 18 51 00 Telefax (47) 73 54 63 87

Title Biodiversity in freshwaters: temporal trends and response to water	Report No 6580-2013	Date October 2013	
chemistry	ICP Waters report 114/2013	Pages Price 65 Free	
	Project No. 0-10300		
Author(s) Gaute Velle, Richard J. Telford, Chris Curtis, Lars Eriksson, Arne Fjellheim, Marina Frolova, Jens Fölster, Natalja	Topic group Acid deposition,	Distribution Open	
Grudule, Godtfred A. Halvorsen, Alan Hildrew, Andreas Hoffmann, Iveta Indriksone, Lenka Kamasová, Jiří Kopáček, Stuart Orton, Pavel Krám, Don T. Monteith, Takaaki Senoo, Ewan M. Shilland, Evžen Stuchlík, Magda-Lena Wiklund, Heleen de Wit, Brit Lisa Skjelkvaale	biodiversity Geographical area Europe and North America	Printed NIVA	

Client(s)	Client ref.
Norwegian Environmental Agency United Nations Economic Commission for Europe (UNECE)	
* · · · · · · · · · · · · · · · · · · ·	

Abstract This report describes trends in biological diversity of benthic invertebrates from acid-sensitive lakes and rivers sampled between 1982 and 2011 in the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. The results indicate an overall increase in species diversity during the study period, especially in the rivers. The increase in biodiversity is correlated with declining sulphate concentrations in surface waters, which in their turn are related to reduced atmospheric deposition of sulphur. The changes in biodiversity could be related chemical recovery of surface waters, where reduced sulphate concentrations are associated with increased pH and lowered aluminium concentrations. Apart from the increased species diversity seen in most sites, the biological recovery trends varied among sites. As a consequence of increased species diversity, the aquatic ecosystems are likely to have a higher resilience against future threats. We can expect an analogous increase in species diversity for comparable sites elsewhere. The improved biodiversity in acid-sensitive waters is in contrast to the world-wide trend of decreasing freshwater species diversity. Our results suggest that international policies to reduce sulphur emissions have promoted a positive development in species diversity of invertebrates in acid-sensitive surface waters.

4 keywords, Norwegian	4 keywords, English		
 Sur nedbør Biodiversitet Akvatisk fauna Overvåking 	 Acid deposition Biodiversity Aquatic fauna Monitoring 		

Helen de bett

Heleen de Wit Project Manager

Ap lay

Thorjørn Larssen Research Director

ISBN 978-82-577-6315-2

CONVENTION ON LONG-RANGE TRANSBOUNDARY AIR POLLUTION

INTERNATIONAL COOPERATIVE PROGRAMME ON ASSESSMENT AND MONITORING EFFECTS OF AIR POLLUTION ON RIVERS AND LAKES

Biodiversity in freshwaters: temporal trends and response to water chemistry

Gaute Velle¹, Richard J. Telford², Chris Curtis^{3,4}, Lars Eriksson⁵, Arne Fjellheim¹, Marina Frolova⁶, Jens Fölster⁵, Natalja Grudule⁶, Godtfred A. Halvorsen¹, Alan Hildrew⁷, Andreas Hoffmann^{8,9}, Iveta Indriksone⁶, Lenka Kamasová¹⁰, Jiří Kopáček¹¹, Stuart Orton⁷, Pavel Krám¹², Don T. Monteith¹³, Takaaki Senoo¹⁰, Ewan M. Shilland³, Evžen Stuchlík¹⁰, Magda-Lena Wiklund⁵, Heleen de Wit¹⁴, Brit Lisa Skjelkvaale¹⁴

¹⁾Laboratory for freshwater ecology and inland fisheries, Uni Research, Bergen, Norway; ²⁾Department of Biology, University of Bergen, Norway; ³⁾ENSIS Ltd, Environmental Change Research Centre, Department of Geography, University College London, United Kingdom; ⁴⁾School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa; ⁵⁾Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden; ⁶⁾Latvian Environment, Geology and Meteorology centre, Riga, Latvia; ⁷⁾School of Biological and Chemical Sciences, Queen Mary University of London, United Kingdom; ⁸⁾University of Applied Sciences Weihenstephan-Triesdorf, Faculty of Environmental Engineering, Germany; ⁹⁾Federal Environment Agency, Section II 2.4 Inland Waters, Germany; ¹⁰⁾Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Czech Republic; ¹¹⁾Biology Centre of the Academy of Sciences of the Czech Republic, Institute of Hydrobiology, České Budějovice, Czech Republic; ¹²⁾Czech Geological Survey, Prague, Czech Republic; ¹³⁾ Centre for Ecology and Hydrology, Lancaster Environment Centre, Lancaster, United Kingdom; ¹⁴⁾ Norwegian Institute for Water Research (NIVA), Oslo, Norway

ICP Waters Programme Subcentre Uni Research AS, P.O.box 7810 N-5020 Bergen, Norway

Preface

The International Cooperative Programme on Assessment and Monitoring of Rivers and Lakes (ICP Waters) was established under the Executive Body of the UNECE Convention on Long-Range Transboundary Air Pollution (CLRTAP) in July 1985. Since then ICP Waters has been an important contributor to document the effects of implementing the Protocols under the Convention. Numerous assessments, workshops, reports and publications covering the effects of long-range transported air pollution has been published over the years.

The ICP Waters Programme Centre is hosted by the Norwegian Institute for Water Research (NIVA), while the Norwegian Environment Agency leads the programme. A programme subcentre is established at Uni Research, University of Bergen. The Programme Centre's work is supported financially by the Norwegian Environment Agency and by the UNECE LTRAP Trust Fund.

The main aim of the ICP Waters Programme is to assess, on a regional basis, the degree and geographical extent of the impact of atmospheric pollution, in particular acidification, on surface waters. ICP Waters depends on existing monitoring programmes for surface water chemistry and biology in the participating countries. Countries contribute to ICP waters on a voluntarily basis. The ICP site network is geographically extensive and includes long-term data series over 30 years. Over twenty countries in Europe and North America participate on a regular basis. The programme yearly conducts chemical and biological intercalibrations to promote harmonisation and quality assurance of monitoring programmes.

In this report we present an analysis of time trends of biological diversity at the ICP Waters sites and their relation to changes in water chemistry. The biological data set includes about 1.6 million benthic macroinvertebrates sampled from 89 European rivers and lakes collected between 1982 and 2011. In addition, data on water chemistry from the same sites and periods are included. Few, if any, comparable previous studies exist at this scale.

The report was prepared by ICP Waters subcentre in Bergen by lead author Gaute Velle. Most numerical analyses were performed by Richard Telford. Data were provided by those responsible for national monitoring programmes on biota and water chemistry. The results are discussed in several steps with the co-authors.

The report was presented at the Task Force meetings in Pallanza in 2012. We would like to thank all those who contributed with comments to the draft report. We are particularly grateful to all those who collected and contributed monitoring data.

Bergen, October 2013

Gaute Velle ICP Waters Programme Subcentre

Contents

Summary	7
1. Introduction	9
1.1 Biodiversity	9
1.2 Biodiversity in freshwaters	10
1.3 Management strategies	10
1.4 Drivers of biodiversity	11
1.5 Measuring biodiversity	11
1.6 Aims of study	13
2. Methods	14
2.1 Study sites	14
2.2 Sampling and species identifications	16
2.3 Consistency in taxonomic resolution and sampling season	17
2.4 Numerical analyses	18
3. Results	19
3.1 Consistency in taxonomic resolution and sampling season	19
3.2 Temporal trends in species diversity (α - diversity)	24
3.3 Assemblage changes over time (β -diversity)	25
3.4 Relationships between water chemistry and species diversity	30
4. Discussion	33
4.1 Taxonomic resolution	33
4.2 Temporal trends in species diversity (α - diversity)	34
4.3 Relationship between environmental variables and species	
diversity	36
4.4 Relationship between indices of species diversity and acidification	
4.5 Sensitivity of species diversity in rivers versus lakes	38
4.6 Assemblage changes over time (β -diversity)	38
5. Implication of findings	39
5.1 Separating what is natural	39
5.2 Extrapolation of results	40
5.3 Ecosystem function	40
5.4 Modelling	41
6. References	42
Appendix A. Study sites	50
Rivers	50
Lakes	52
Appendix B. – Taxonomic consistency	54
Norway lakes	54
Sweden lakes	54

UK lakes	54
German rivers	55
Latvia	55
Norway rivers	55
Czech Republic	56
Sweden rivers	56
UK rivers	56
Appendix C. – Diversity details	57
a-diversity of rivers	58
a-diversity of lakes	59
β -diversity of the sites that are not shown in main text	62
Appendix D. Reports and publications from ICP Waters	64

Summary

In this ICP Waters report, we provide results from analyses on the species diversity of benthic invertebrates sampled in freshwater monitoring sites from the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. The data includes about 1.6 million benthic macroinvertebrates from 5010 samples in 55 rivers and 34 lakes collected between 1982 and 2011. In addition, data on water chemistry from the same sites and periods are included, where such data exist. The study sites were chosen as part of national monitoring programmes and most represent type sites of nutrient poor waters that have been influenced by long-range air pollution leading to acidification. To our knowledge, no comparable studies exist at this scale.

The results from the analysis of water chemistry show that the concentration of sulphate has decreased, while pH and buffering capacity (ANC) have increased. This is in line with previous trend analyses of water chemistry at ICP Waters sites and confirms on-going chemical recovery, as a response to the decrease in long-range transboundary air pollution. Improved chemical status has been associated with a restoring ecological status over the last two decades, as measured by acidification indices. Such acidification indices are based on acid-sensitive taxa in a sample, while the species diversity indices are based on all taxa in a sample. In terms of species diversity, the response will vary according to the initial impact, natural variation and according to biological processes, such as competition and predation. This suggests that acidification indices and species diversity indices are not necessarily correlated, which is confirmed by our results.

According to our results, a majority of the rivers and lakes (70 of 89 sites) show a net increase in species diversity (exponential of Shannon's diversity index), albeit the increase is not statistically significant at all sites. This increase is statistically significant for rivers in Germany, Sweden and Latvia. The species diversity of lakes has increased to a smaller extent than the diversity of rivers and only the littoral zone of Swedish lakes shows a significant increase. There was a significant decrease in species diversity in the sublittoral of the Swedish lakes. This decline could be associated with increasing concentrations of dissolved organic carbon (DOC) which result in increases in the colour of lake water. Future records are needed to find whether the non-significant trends can be considered as natural variation or as significant changes. The differences in responses between lakes and rivers could be related to habitat stability where rivers experience more heterogeneous environmental conditions than lakes and lakes therefore are more resilient to changes. This may imply that the biota of rivers is more adapted to a fast re-colonization and that the recovery in the lakes is delayed, or that the biota in the lakes was less influenced by the acidification. In addition, a larger fraction of the taxa are identified to species level in rivers compared to lakes. The implication is that the biota of rivers apparently is more sensitive to changes than the biota of lakes.

The data-analysis suggests that improved species diversity and declining sulphate are correlated. Reductions in sulphate concentrations in acid-sensitive catchments, resulting from reductions in sulphur deposition, are a driver of changes in pH and aluminium, both of which are associated with toxic effects on aquatic biota. In terms of community response, the timing of the recovery and the biological characteristics of the recovery is nonlinear and non-comparable among sites. This suggests that future biological recovery to acidification will not show a universal pattern across sites. Globally, the species diversity of freshwaters is declining, while the species diversity of the sites in the present study is increasing. Adequate species diversity data on invertebrate populations are lacking from the pre-industrial period and from the period of strongest acidification during the 1970s and 1980s. Documented loss of fish species due to acidification is clear evidence of the loss of biodiversity, and macroinvertebrates may exhibit the same pattern. The improvement of species diversity shown in this report suggests a biological recovery in response to improved water chemistry. We can expect a similar increase in species diversity for comparable acid sensitive waters elsewhere. The biological recovery progress varies among sites, and the strongest recovery probably occurred before monitoring started at some sites that have been heavily impacted by acidification, such as in the Czech rivers. The on-going recovery in species diversity recovery indicates dynamic changes in populations and it is unlikely that species diversity is yet back to preindustrial values.

Following increased species diversity, the ecosystems might be expected to be more resistant towards anticipated threats, such as climate change or habitat degradation. It still seems that the species diversity in rivers is more sensitive to changes in environmental conditions than in lakes, highlighting the importance of careful management of rivers.

This international, quality controlled long term monitoring of water chemistry and biota in acidsensitive waters have been important in tracking changes in the diversity of invertebrates in these ecosystems, and their possible causes, i.e. air pollution. Reduction in the emissions of acidifying pollutants has been followed by a positive development in the species diversity of acid-sensitive freshwaters, in sharp contrast to the global trend of decreasing freshwater species diversity.

1. Introduction

Pollution that causes acidification has seriously influenced the biota of many European regions. In Norway, detrimental effects on Atlantic salmon (Salmo salar L) and brown trout (Salmo trutta L.) had been reported nearly one century ago (Huitfeldt-Kaas, 1922). Detrimental effects on the most sensitive benthic invertebrates likely began prior to the effects on fish (Raddum et al., 1984). Now, acidifying components in precipitation, surface water chemistry and biota are monitored in international programmes under the Convention on Lon-range Transboundary Air pollution (CLRTAP). Monitoring programmes indicate a reduction in atmospheric pollution since the late 1980's, causing improved water quality and improved ecological state in a broad range of geographical areas (Evans et al., 2001; Halvorsen et al., 2003; Hesthagen et al., 2011; Johnson and Angeler, 2010; Lento et al., 2012; Monteith et al., 2005; Stendera and Johnson, 2008; Stoddard et al., 1999). The biological recovery typically includes reappearance, followed by a modest or pronounced increase in acid-sensitive taxa (Hesthagen et al., 2011; Raddum and Fjellheim, 1995). In this report, we assess for the first time overall trends in biological diversity at monitoring sites since the start of the monitoring. We also assess the influence of water chemistry on the biological diversity.

1.1 Biodiversity

Biological diversity, or biodiversity, is a key concept used by scientists, policy makers and laymen. Biodiversity ranges from genetic diversity to the diversity of ecosystems in landscapes (Millennium Ecosystem Assessment 2005; Purvis and Hector, 2000). According to Article 2 of the Convention on Biological Diversity (http://www.cbd.int/convention/articles/default.shtml?a=cbd-02), the term "biodiversity" represents the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

Biodiversity may have important consequences for ecosystem processes, because species types and numbers determine the functional traits in the ecosystem as well as goods and services crucial for human well-being (Chapin Iii et al., 2000; Hooper et al., 2005). Human activities are now responsible for a species loss 100 to 1000 times greater than normal background rates (Rockstrom et al., 2009; UN, 2005). The main causes for the present extinctions include altered land use and over-exploitation of resources, habitat loss and habitat fragmentation, as well as species introduction and pollution. Superimposed on these stressors, climate change now exerts some hitherto uncertain pressure on biodiversity, either directly or indirectly (Heller and Zavaleta, 2009; Mantyka-pringle et al., 2012). As a response to the threats, the partners to the Convention on Biological Diversity committed themselves in 2002 to achieve, by 2010, a significant reduction in the current rate of loss of biodiversity at the global, regional and national level. This target was not met (Spyropoulou et al., 2010) and the loss of biodiversity continues. In October 2010, governments agreed to a Strategic Plan for Biodiversity 2011-2020 aiming at halting and eventually reversing the loss of biodiversity of the planet by 2020. To

build support and momentum for this task, the United Nations General Assembly at its 65th session declared the period 2011-2020 to be "The United Nations Decade on Biodiversity".

1.2 Biodiversity in freshwaters

Biodiversity is not evenly distributed among ecosystems. Compared to its volume or surface area, the biodiversity of freshwaters is high compared to the rest of the Earth. Freshwater covers about 0.8% of the Earth's surface yet includes about 6% of all described species and 35% of all vertebrate species (Gleick, 1996; Hawksworth, 1995; Stendera et al., 2012). Freshwater bodies are especially influenced by human perturbations, and freshwaters may be the most endangered ecosystems on Earth (Dudgeon et al., 2006; Sala et al., 2000). Even lakes long considered as pristine sanctuaries at high altitudes- and latitudes are now more or less impacted (Smol et al., 2005). This is alarming since impacted waters are transformed into less desired states that threaten biodiversity and ecosystem services, including supply of water, fishing, recreation and tourism (Scheffer et al., 2001). In North America, it has been estimated that 40% of all freshwater fish species are at peril (Jelks et al., 2008). The number of unknown species of invertebrates is large and inventories and monitoring programmes of freshwaters are lacking in many parts of the world. The implication is that the number of freshwater invertebrate species that are threatened by extinction is largely unknown. The direct influence of decreasing biodiversity on freshwater ecosystems is still not clear. At least two key influences that affect ecosystem processes can be distinguished: (1) ecosystem resilience may be reduced (Elmqvist et al., 2003), and (2) the rates of ecosystem processes will be modified (Dudgeon et al., 2006; Hooper et al., 2005). A 'healthy' ecosystem can be defined as sustainable system – that is, it has the ability to maintain its structure (organization) and function (vigor) over time in the face of external stress (resilience) (Costanza and Mageau, 1999).

1.3 Management strategies

The major types of stressors that may combine to affect freshwater ecosystems adversely include overexploitation, (water) pollution, habitat degradation, species invasion and flow modification (Dudgeon et al., 2006). Superimposed on these stressors, climate change exerts an unknown pressure on biodiversity, either directly or indirectly (Currie et al., 2004; Heller and Zavaleta, 2009; Mantykapringle et al., 2012; Mayhew et al., 2012). Responding to the severity of the situation, ecosystem managers facing this "terra incognita" (Steffen et al., 2007) aim at developing management strategies to maintain the goods and services of freshwaters. These management strategies should include assessments of human impact, in order to separate natural phenomena from human-induced influence. At a time of species-loss, in-depth knowledge about biodiversity and its threats is necessary for decisive for successful management.

The threats to freshwaters were especially evident during the second half of the last century, when the influence of acidification caused by long-range transported air pollutants initiated biodiversity loss and alterations of ecosystem processes (Schindler, 1988). Fortunately, management strategies aimed at targeting threats from acid deposition have now caused a reversing trend of the negative impacts for

many sites in Europe and North America. An important part of the policy to combat acid deposition was to establish monitoring programmes, in order to create 'effect-based' policy, i.e. policy to reduce acidifying emissions where it mattered most, based on documented dose-effect relationships. Such monitoring assesses the current condition of ecosystems relative to their past status and has been important in tracking the trajectory of ecosystems and pollution (e.g., Skjelkvaale and de Wit, 2011). With the benefit of hindsight, monitoring should have begun before the onset of anthropogenic acidification, thereby providing indisputable data on pre-disturbance states. In reality, monitoring programmes were initiated only after belated recognition of the effects of acid deposition and rarely started before the 1980's, i.e., at a time when susceptible waters had already been heavily influenced by acidification. Despite national and international policy implementation to reduce atmospheric acid deposition, evidence of ecological recovery is still equivocal or impeded (Angeler and Johnson, 2012; Lento et al., 2012; Monteith et al., 2005; Murphy et al., in press). The influence on biodiversity and ecosystem function is particularly poorly understood (Johnson and Angeler, 2010; Ledger and Hildrew, 2005) and it is largely unknown whether ecosystem recovery includes a return to a biodiversity and ecological state similar to pre-acidified conditions or to alternate states.

1.4 Drivers of biodiversity

A critical issue for lake management is to unravel the factors controlling biodiversity. The main threats to freshwaters, including over-exploitation, water pollution, habitat degradation, species invasion and flow modification, do reduce biodiversity. Apart from perturbations caused by humans, however, patterns of species richness are correlated with latitudinal and other natural gradients (Hawkins et al., 2003; Wright et al., 1993). Rohde (1999) concluded that latitudinal gradients in species diversity result from effective evolutionary time modulated by several factors, such as temperature and energy input. At a smaller scale, factors controlling biodiversity include interactions among many abiotic and biotic variables, such as disturbance and stream stability, eutrophication, food availability and available area (Lods-Crozet et al., 2001; Solimini et al., 2008; Stendera et al., 2012). For aquatic insects, species richness and assemblage composition are also strongly correlated with habitat size and acidity (Heino, 2009). The relationship between species richness and acidity also implies that biodiversity can be expected to increase as atmospheric pollution is reduced.

1.5 Measuring biodiversity

An ideal biodiversity index is able to reduce complex information on structure and abundance to simple numerical metrics. However, it is important to be aware of two main limitations to the concept of biodiversity: (1) the term is artificial implying that biodiversity not is an intrinsic property in nature and (2) biodiversity is a simplification of nature and it is necessary to consider that information is lost when complex processes are reduced to a single number (Hurlbert, 1971). Since biodiversity has many meanings and is generally poorly understood, the term is inevitably used inconsistently and often imprecisely. In order to avoid misunderstandings, here we restrict ourselves to species diversity – a major component of biodiversity and with a clear scientific definition.

In his development of a conceptual family of species diversity indices, Whittaker (1960) determined the total diversity in the landscape (γ -diversity) by the diversity at one site (α -diversity) and the diversity difference among sites or with time (β -diversity). For the basic unit of biological classification, the species, α -diversity is expressed as a function of the number of species and their frequency (Chapin Iii et al., 2000; Tuomisto, 2010). The present study focuses on α -diversity and β -diversity. In addition to the conceptual family, another family of biodiversity indices include so-called functional diversity metrics. Functional diversity reflects the biological complexity of the ecosystem expressed by important biological traits (Heino, 2005, 2008; Schleuter et al., 2010). Such traits could include feeding mode, food source, mode of mobility, size at maturity, life cycle length etc. A change in these traits over space or time gives direct information about ecological processes

Several indices exist for measuring α -diversity, each with its own set of limitations and advantages. All indices also come with a set of assumptions. These assumptions should aid in the selection of species diversity index according to the data at hand, so that they are violated as little as possible. The indices weight the number of species and their frequency differently, but most are correlated within a given community (DeBenedictis, 1973). The most basic diversity metric is based solely on the total number of species collected (species richness). Although richness is an intuitive measure of species diversity, being easy to understand, many ecologists prefer to avoid using it for a number of reasons. Species richness is correlated with the sampling effort in the field (Bady et al., 2005; Jost, 2006; Lande, 1996), so sampling effort should be standardized before richness can be compared within sites or among sites. Common and rare taxa are given equal weight in species richness, which gives dubious ecological meaning and also leads to a measure of species diversity that is slow to converge to a definite value. Consequently, repeated samples from an ecosystem often show a high variability in species richness compared to other indices of species diversity.

Researchers have pointed out that estimation of species diversity not is straightforward because of bias due to varying sample size (Birks and Line, 1992) and suggest that rarefaction analyses should be used when assessing it. In rarefaction, the sample size is standardized by weighting the contribution of each species by its abundance or occurrence (Birks and Line, 1992; Walker et al., 2008). Estimation of species richness by rarefaction has many advantages. However, rarefaction assumes that the number of occurrences of a species reflects the sampling intensity, implying that rarefaction curves will be skewed if the sampling effort is not comparable among sites. Also, rarefaction is problematic if some of the samples are very small.

Most other diversity-indices, such as the Simpson, Shannon, or Berger-Parker indices include species proportions or frequencies in their calculation. The advantage is that common and rare taxa have unequal weight, so that biological communities are differentiated more effectively. The weighting differs among indices, where some weigh common taxa, while others weight rare taxa. Compared to species richness, such indices may at first sight seem difficult to interpret. However, this is overcome by converting the indices into effective number of species measured in species units. The effective

number of species is the number of equally-common species required to give a particular value of the index (Jost, 2006).

1.6 Aims of study

In the present study, we have used extensive monitoring data on benthic macroinvertebrates (Figure 1) and water chemistry sampled from mid-1980 and up to the present. Participating countries in this study include the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. Importantly, all countries participate in both hydrochemical and macroivertebrate intercomparison schemes that ensure international comparability.

Our primary objectives have been to use robust numerical techniques and a suitable measure of biodiversity for the data at hand to (1) record trends in the species diversity of benthic macroinvertebrates from the beginning of the monitoring period to the present, (2) search for common trends in α - diversity among sites, (3) examine α -diversity in the light of the external chemical stressors, especially chemical variables related to acidification and (4) search for common community changes among sites (temporal β -diversity). In future studies, we hope to also focus on the influence of temperature on α -diversity, to analyse the functional diversity of communities and to model α -diversity as a function of future scenarios of temperature and water chemistry.



Figure 1. Benthic invertebrates from Norwegian rivers. From left to right the stonefly Diura nanseni, the caddisfly Potamophylax sp. and the mayfly Baetis rhodani. Photos by A. Fjellheim (Uni Research).

2. Methods

2.1 Study sites

Study sites include lakes and rivers from the Czech Republic, Germany, Latvia, Norway, Sweden and UK (Table 1 and Table 2, APPENDIX A – Study sites). The full data set includes about 1.6 million benthic macroinvertebrates from 5010 samples in 55 rivers and 34 lakes collected between 1982 and 2011 (Figures 1-3, Tables 1-2). These sites form part of national biological- and chemical monitoring programmes in running and standing freshwaters (Halvorsen et al., 2002; Horecký et al., 2002; Horecký et al., 2006; Horecký et al., 2013; Johnson and Goedkoop, 2007; Kernan et al., 2010; Schaumburg et al., 2008). The bedrock varies among sampling regions, but apart from Latvia, most sites are in acid-sensitive bedrock consisting of gneiss, granite or quartzite. The Latvian sites are situated on claystone including smaller fractions of dolomite and gypsum. In terms of vegetation, the northernmost sites are situated in boreal vegetation and the southernmost sites are situated in cool temperate vegetation. Some of the sites, especially in Germany and Latvia, are placed in small stands of forest surrounded by farmland. In addition to biological samples, the data include water chemistry measurements. A combined data set was compiled that includes paired invertebrate samples and chemistry samples (Table 1 and Table 2).

Table 1. Samples from rivers with number of biological samples, number of sub-samples, average sample size,
number of paired chemistry samples and sampling period. All biological samples have been taken by kick-
sampling. *The Norwegian rivers include a total of 59 sampling stations.

	Number of Rivers	Biological samples	Sub- samples	Average sample size	Chemical samples	Sampling period
Czech Republic	4	58	1	1102	57	1999-2011
Germany	29	1074	1		1074	1982-2010
Latvia	5	46	1	150	38	1997-2011
Norway	3*	2255	1	217	284	1987-2010
Sweden	6	91	5 or 6	236	91	1985-2011
UK	11	234	3 or 5	1312	216	1988-2010

Table 2. Samples from lakes with number of biological samples, number of sub-samples, average sample size, number of paired chemistry samples and sampling period. Note that the Swedish littoral, sublittoral and profundal samples were taken from the same seven lakes. Grab samples were taken by use of an Ekman grab.

	Lakes	Biological samples	Sub- samples	Sampling method	Average sample size	Chemical samples	Sampling period
Norway	20	558	1	Kick	282	378	1997-2010
Sweden littoral	7	179	5	Kick	195	179	1986-2010
Sweden sublittoral	7	155	5	Grab	227	155	1989-2010
Sweden profundal	7	228	5	Grab	183	195	1986-2010
UK	6	132	3-7	Kick	442	130	1988-2010

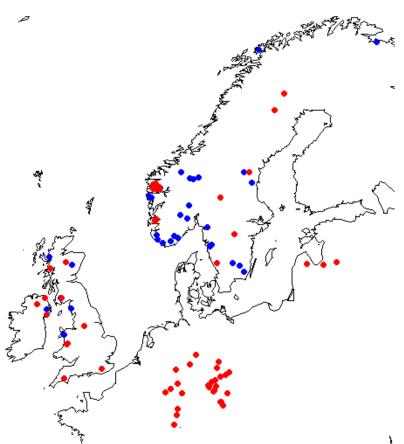


Figure 2. Sampling sites. Red dots denote running waters and blue dots denote standing waters. *There are a total of 112 sampling sites in rivers and 48 sampling sites in lakes.*



Figure 3. Sampling in the upper reaches of River Gaular in Norway. This site is typical for the Norwegian rivers. Photo by P. Fagard (Uni Research).

Water chemistry was sampled at the biological sampling stations, but not at every sampling station and not for all corresponding sampling-times. As criteria for the inclusion of water samples, the samples should be from the biological sampling stations and be sampled not more than two weeks after, or six weeks before, the time of biology sampling. The time window was skewed towards chemistry samples preceding the biological sampling assuming that the assemblages had indeed experienced past chemistry, but that the influence of an unknown future chemistry was uncertain. For the same reason, when more than one chemistry sampling date could be paired with a biological sample, the date preceding the time of the invertebrate sampling was preferred. The combined data set includes 2797 samples with about 950 000 benthic invertebrates and about 35 000 data entries on water chemistry. Chemical variables includes pH, conductivity, alkalinity, calcium (Ca2+), magnesium (Mg2+), potassium (K+), sodium (Na+), chloride (Cl-), sulphate (SO42-), total nitrogen (TotN), nitrate (NO3-), total organic carbon (TOC), hydrogen (H+) and labile aluminium (LAL). Acid-neutralizing capacity (ANC) was calculated as (Ca+Mg+Na+K+NH4) - (Cl+SO4+NO3). For a detailed description of measured water chemistry, see Skjelkvaale and de Wit (2011). For a full list of sites, including name, geographical coordinates, altitude, lake depth, lake area, number of biological samples, number of chemical samples and sampling period, see APPENDIX A - Study sites.

2.2 Sampling and species identifications

Most invertebrates were collected by kick sampling (Frost et al., 1971), following the ICP-Waters manual (Wathne et al., 2010). In this procedure, the substrate is disturbed and collected in a 0.25 mm mesh net (Figure 4). An Ekman grab was used in the Swedish sublittoral- and profundal lake sites. The sampling interval varied among sites and years with an average of about 1.5 samples per sampling station per year from the time most monitoring programmes opened in 1987 and up to the present.



Figure 4. Kick-sampling for benthic invertebrates in a Norwegian river. Photo by G.Velle (Uni Research).

Each sample was sorted under a stereo microscope in the laboratory, and macroinvertebrates subsequently identified. Leeches (Hirudinea), molluscs (Mollusca), mayflies (Ephemeroptera), stoneflies (Plecoptera), caddis flies (Trichoptera), water beetles (Coleoptera), dragon flies (Odonata) and water bugs (Hemiptera) were identified to the lowest possible taxon, i.e. species or genus, whereas most other taxa were identified to family or genus. The zoobenthos were identified with the use of extensive national and international keys, such as Askew (1988), Lillehammer (1988), Nilsson (1996) and Wallace et al. (1990).

2.3 Consistency in taxonomic resolution and sampling season

The specimens were identified by local experts and the data are of high quality. The data contributors have also participated in annual ICP-waters biological- and chemical inter-calibrations (e.g., Dahl and Hagebø, 2011; Fjellheim et al., 2011; Raddum, 1993). The inter-calibration focuses on improving the quality of work at the national laboratories as well as harmonisation of methods and databases. The biological inter-calibration focusses on the taxonomic skills of the participants and each participating laboratory identifies mixed samples of invertebrates. Based on the fraction of specimens correctly

identified to genus or species, and on the fraction of specimen identified, the laboratory is given a quality assurance index. A score above 80 is regarded as good. The score was around 80 during the first years of the inter-calibrations and has now stabilized at about 95 (e.g., Fjellheim et al., 2011; Raddum, 1993), indicating taxonomic excellence.

Despite a standardized sampling procedure and high taxonomic accuracy, it remains possible that taxonomic resolution has varied over the last 30 years of monitoring. Since we are analysing trends in species diversity over time and not comparing the absolute diversity among sites, taxonomic resolution does not need to be standardized among sites. However, if the taxonomic resolution has varied systematically at any one site, then the trends in species diversity may be biased. Inevitably, many taxa are sometimes identified to species and other times to a broader taxonomic level. Such inconsistencies could be caused by varying larval size at the time of sampling where small specimens cannot be identified to species. In order to test for systematic inconsistencies, we first registered the lowest taxonomic level that supra-specific taxa were identified to. Then, in a second step, we plotted the fraction of specimens identified to the lowest taxonomic level (usually species) in each sample against time. For taxa that sometimes are identified to species and sometimes to a broader taxonomic resolution, there should not be a relationship between taxonomic resolution and time. In order to correct for inconsistencies, the taxonomy was amended to a broader level by merging taxa with inconsistency taxonomy until any trend in taxonomic resolution disappeared.

Time of sampling during the year may also influence species diversity. A great number of taxa are usually found during autumn than during spring. Consistent sampling will not compromise diversity (e.g., samples are collected in spring and autumn every year). However, inconsistent changes in sampling season, e.g., a change from all autumn sampling to all spring sampling, may cause changes in diversity. In order to detect any inconsistency in time of sampling, the sampling quarter was recorded for all samples at any one site and plotted against time and against diversity.

2.4 Numerical analyses

As a measure of α -diversity, we have adopted the exponential (exp) of the Shannon entropy (N1). The mathematical formula for N1 is used in information statistics as a general measure of uncertainty and diversity. When used as an index of species diversity, it translates into effective number of species measured in species units. The exponential of N1 is then calculated as:

$$N1 = \exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right)$$
(1)

where p is the relative abundance of taxon i in the sample and ln is the natural logarithm. N1 is comparable among unequal-sized communities since it converges quickly to a stable value, weighs all species in proportion to their frequency in the sample and is weakly influences by common or rare species (Jost, 2006). N1 assumes that all individuals are sampled randomly, that the population is indefinitely large (effectively infinite) and that all species in the community are represented. It may be

difficult to justify these assumptions for many communities, particularly very diverse communities. Moreover, the assumptions indicate that incomplete sampling may cause bias. Nevertheless, we still assume that any abs caused by potential violations of the assumptions are slight and that this is the most appropriate index to use in the present study. The sample size in the study varies by three orders of magnitude, implying that rarefaction is not feasible.

Linear trends in diversity for each site and for each country were assessed by use of linear mixed effect models (lme) with random intercept and slope, and tested for statistical significance. The species diversity trends (negative or positive) from a linear least squares model for each site were also plotted on a map. Non-linear methods (generalized additive models, GAM) were used for sites that included more than ten samples. The number of degrees of freedom in GAM was set to ten.

As a measure of the difference in community composition over time at any one site (β -diversity), we have used non metric multidimensional scaling (NMDS). NMDS is an ordination technique that visualizes the level of similarity among species assemblages. Unlike other ordination methods, NMDS makes few assumptions about the nature of the data, e.g. about linearity or unimodality. In a NMDS diagram, proximity reflects similarity in species composition among samples. We used Bray-Curtis as a distance metric.

The influence of chemical variables on species diversity (N1) was also tested. In such an analysis, it is not straightforward to run the full dataset into one joint analysis, i.e., as a multiple regression with water chemistry as independent variable and species diversity as dependent variable. The range in any environmental variable of interest varies among sites where both high and low values may be associated with high and low diversity. Further, the biological sensitivity to acidification varies among regions of Europe (Raddum and Skjelkvale, 2001), also for single species (Moe et al., 2010), suggesting site-specific analysis. Hence, we have assessed the relationship at each site independently and summed up the overall findings. The correlation was assessed by use of lme and tested for statistical significance. Significance was corrected for multiple tests with Bonferroni correction. Many of the chemical variables, such as some major ions, are closely correlated with one another, and some chemical variables are derivatives of others. In addition, not all chemical variables were measured at every site. In order to reduce collinearity and noise, only six chemical variables (pH, SO4, NO3, NH4, ANC and conductivity) were retained in the analyses.

All numerical analyses were performed using the statistical package R (R development core team 2010) using several statistical libraries (RODBC, vegan, maps, mapdata, mgsv, MASS and nlme).

3. Results

3.1 Consistency in taxonomic resolution and sampling season

For several regions, the fraction of the zoobenthos identified to species compared to that resolved more coarsely has changed considerably since monitoring began (Figures 5 and 6, Table 3). This altered taxonomic resolution is most pronounced in the German streams, in the Norwegian rivers, in the Czech inflow streams, in the sublittoral of Swedish lakes and in UK lakes. For these sites, uncorrected trends in species diversity can be expected to be more or less biased.

Table 3. The correlation (linear or non-linear, whichever is highest) between taxonomic resolution and time for the original data and in the amended data subsequent to taxonomic correction. Trends in this relationship can lead to biased species diversity measures. In order to remove this potential bias, taxa in the original dataset were merged until the correlation between taxonomic resolution and time in the amended dataset was close to zero. Only taxa that influenced R^2 were merged. For a complete list of merged taxa, see APPENDIX B – Taxonomic consistency. * indicates significance at p < 0.05.

		Taxonomic resolutio	n versus time (R^2)
	Country	Original dataset	Amended dataset
Streams	Czech Republic	0.35*	0.001
	Germany	0.081*	0.006
	Sweden	0.041*	0.006
	UK	0.002	0.002
	Latvia	0.05	0.005
	Norway: Vikedal	0.027	0.027
	Norway: Gaula	0.041	0.022
	Norway: Nausta	0.031	0.031
Lakes	Norway	0.041	0.007
	Sweden: littoral	0.260*	0.06
	Sweden: sublittoral	0.093*	0.016
	Sweden: profundal	0.015	0.015
	UK	0.232*	0.026
Average		0.1*	0.017

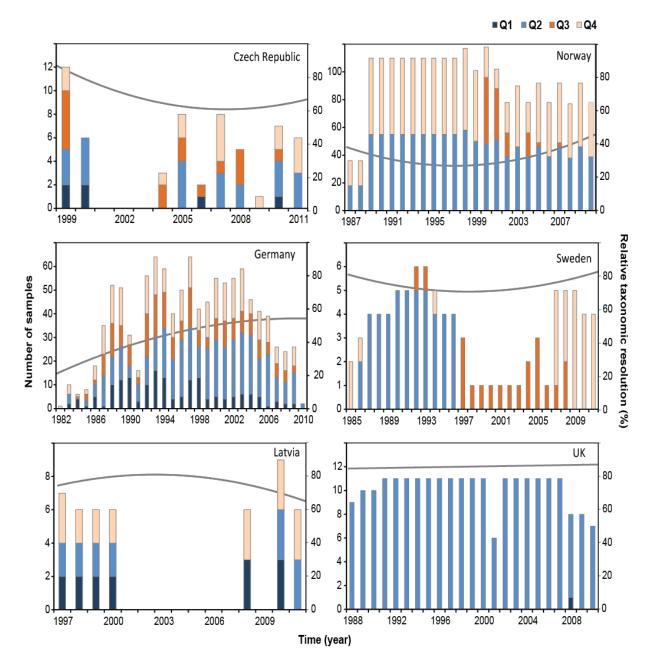


Figure 5. Biological samples from rivers with potential sources of biased species diversity estimates, including consistency in sampling season and taxonomic resolution over time. The number of samples (left-hand scale) is shown as bars and indicates the quarter of sampling (Q1 - Q4) during the year. The grey line indicates the taxonomic resolution (right-hand scale) in each study region based on the raw biological data. The taxonomic resolution is the average fraction of specimens identified to the lowest taxonomic level (usually species) in each country (absolute numbers are not comparable among sites). Only taxa that sometimes were identified to species and sometimes to a coarser taxonomic level were included. In an amended dataset, such taxa were merged to a coarser unit so that the relative taxonomic resolution became a horizontal line (Table 3, see also APPENDIX B – Taxonomic consistency).

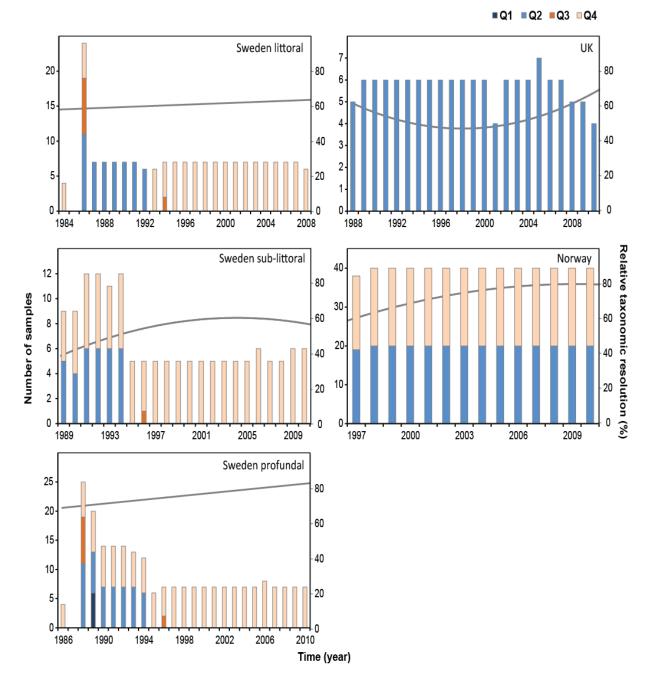


Figure 6. Biological samples from lakes with potential sources of biased species diversity estimates, including consistency in sampling season and taxonomic resolution over time. The number of samples (left-hand scale) is shown as bars and indicates the quarter of sampling (Q1 - Q4) during the year. The grey line indicates the taxonomic resolution (right-hand scale) in each study region based on the raw biological data. The taxonomic resolution is the average fraction of specimens identified to the lowest taxonomic level (usually species) in each country (absolute numbers are not comparable among sites). Only taxa that sometimes were identified to species and sometimes to a coarser taxonomic level were included. In an amended dataset, such taxa were merged to a coarser unit so that the relative taxonomic resolution became a horizontal line (Table 3, see also APPENDIX B – Taxonomic consistency).

In general, the taxonomic resolution has remained stable or increased since 2000-2002, consistent with the enhanced focus on taxonomic harmonization procedures and taxonomic skills among members of ICP Waters. Since that time, inter-calibration was performed annually. Data from sites with inconsistent taxonomic resolution were reduced to a coarser taxonomic level prior to numerical analysis (Table 3). We only present diversity results from the corrected dataset.

The number of samples acquired during any one year can be seen from Figures 5 and 6. Some regions show a decreasing number of samples towards the present, e.g., in rivers from Norway, Germany and the UK, and in lakes from UK. Reduced funding has caused this decline.

With regard to sampling season, most regions are sampled consistently in spring (UK), in spring and autumn (Norway), or at a higher frequency (Czech Republic, Latvia and Germany). There was a shift from spring to autumn sampling for Swedish rivers and lakes in the mid-1990s (Figures 5 and 6).

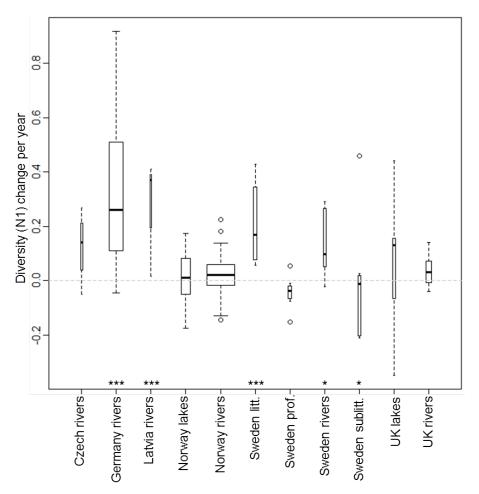


Figure 7. Boxplot showing overall trends in species diversity for all rivers and lakes. The box marks the 25th and 75th percentile and the median, the whiskers mark the interquartile range and the circles denote outliers. The width of the box indicates the number of samples. Values above the zero line denote an increase in diversity and values below zero denote a decrease in diversity. Statistically significant trends at the national level are marked with *, where * p < 0.05 and *** p < 0.001.

3.2 Temporal trends in species diversity (α- diversity)

Most regions have shown some increase in α - diversity over the last 25 years (Figure 7). Diversity has increased significantly in the German rivers, Swedish rivers, Latvian rivers and in the littoral of Swedish lakes (Figures 9 and 10). There has been a significant decrease in species diversity in the sublittoral of Swedish lakes. Overall, it seems that the increase in diversity is more pronounced for rivers than for lakes. Non-linear trends for sites with a significant change in diversity are shown in Figure 10, while raw data and non-linear trends for all sites can be found in APPENDIX C – diversity details. There is no clear influence of altered sampling season on the species diversity of the Swedish lakes, while the Swedish rivers show a break point concurring with the shift. Still, it seems this break point does not alter the diversity trend since there was an increase before and after the shift.

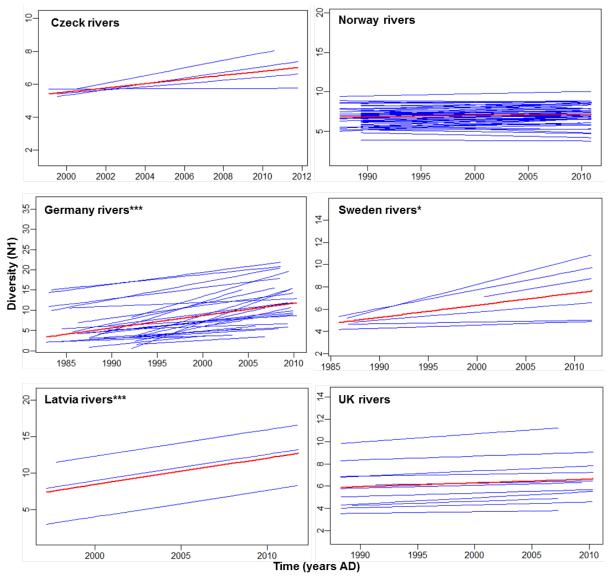
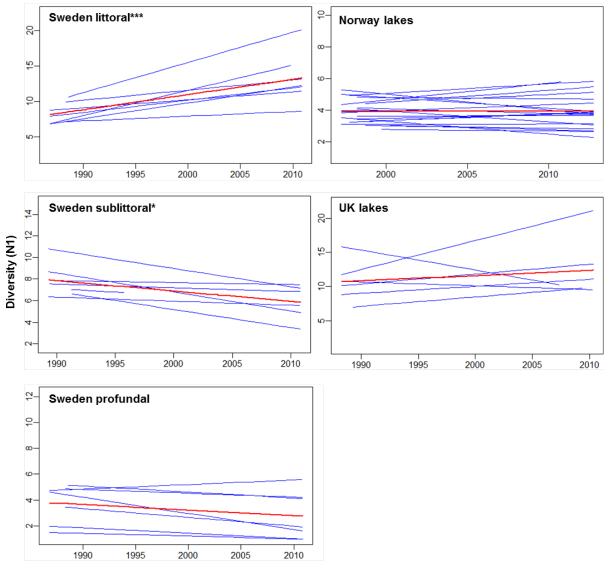


Figure 8. Species diversity (Shannon $N1_{exp}$) for zoobenthos in rivers from The Czech Republic, Germany, Latvia, Norway, Sweden and the UK. The blue lines represent the signal in single rivers (measured by linear mixed effect models), whereas the red line represents the overall signal for each country. * denotes the significance level of the diversity change, where * p<0.05 and *** p< 0.001.



Time (years AD)

Figure 9. Species diversity (Shannon $N1_{exp}$) for zoobenthos in lakes from Sweden, Norway and the UK. The blue lines represent the signal in single lakes (measured by lme), whereas the red line represents the overall signal for each country. * denotes the significance level of the diversity change, where * p<0.05 and *** p< 0.001. The Swedish littoral, sublittoral and profundal samples were taken from the same lakes.

3.3 Assemblage changes over time (β-diversity)

The biological assemblages show little consistent patterns of change over time and much intern-annual variability, with the exception of the littoral in Swedish lakes (Figure 11). Here, the assemblages have changed consistently since the 1980s and towards the present. This implies that most sub-littoral Swedish taxa have undergone similar changes at all sites, e.g., either decreasing or increasing abundance. The Swedish sublittoral assemblages show some directional changes, but not as clear as the littoral samples. There are no clear changes in the profundal of the Swedish lakes or for any other datasets. For these sites, the NMDS indicates that the taxa composition may have changed, but not in unison and not to any new states. The assemblages are more or less the same now as they were in the 80s or 90s.

NIVA 6580-2013

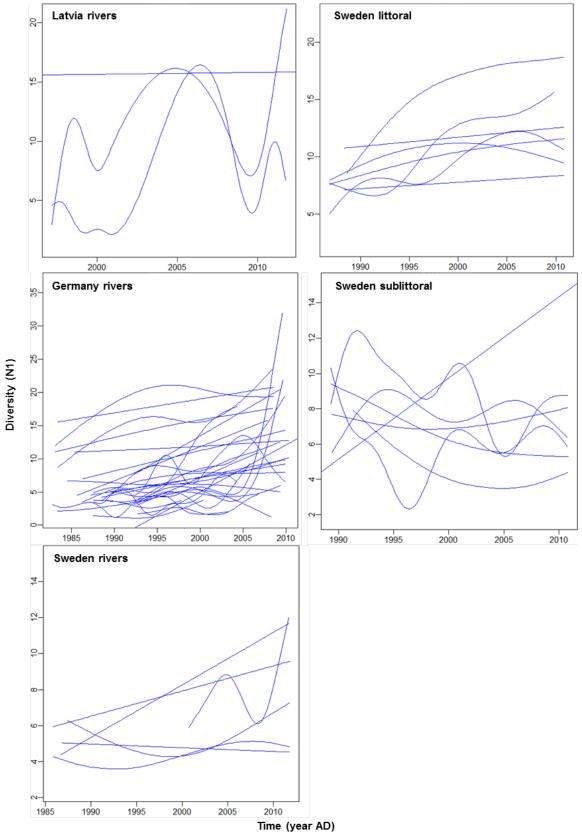
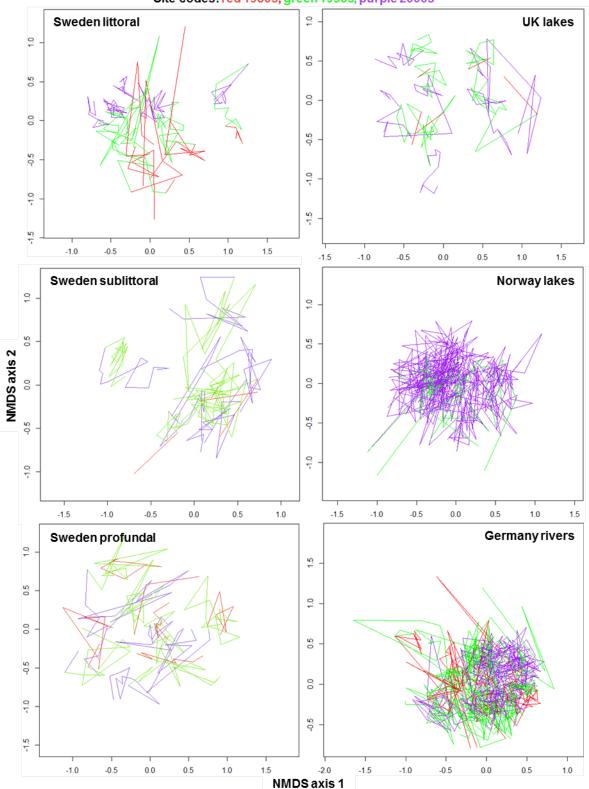


Figure 10. Non-linear (GAM) curve-fits of species diversity (Shannon $N1_{exp}$) for regions with a statistical significant change in diversity. For all regions, see APPENDIX C – diversity details.



Site codes: red 1980s, green 1990s, purple 2000s

Figure 11. β -diversity analysed by non-metric multidimensional scaling (NMDS) in selected countries. The trajectories (lines) show assemblage changes from the 1980s and towards the present with colour codes representing decade of sampling. Closely placed samples have a similar species composition. Only the littoral of Swedish lakes show directional patterns of change, whereas for the other regions, the assemblages change seemingly at random. For missing plots, see APPENDIX C – diversity details.

3.4 Relationships between water chemistry and species diversity

A chemical recovery was evident in the study sites. The most pronounced changes include decreased concentration of SO4 (sulphate), increased pH and increased ANC (Figure 12 and 13). For Latvia, pH has remained stable. The Latvian sites are situated on limestone and have not experienced acidification. For these sites, the reduction in SO4 is unlikely to be related to a reduced sulphate deposition, because deposition adds only a fraction to the background sulphate from the bedrock. Probably, some other factors play a role, such as climate, drought or agriculture.

Sulphate is the most pronounced chemical cue related to species diversity in the rivers as there is a statistically significant negative correlation between diversity and sulphate in 17 of 61 sites. (Figure 12, Table 4). Eleven of the rivers show a positive correlation between ANC and diversity. The relationship in lakes is noisy where a chemical parameter seemingly can influence diversity positively and negatively (Table 5), suggesting it is not causational. For example, there is a positive correlation between sulphate and diversity for three sites and a negative correlation for five sites.

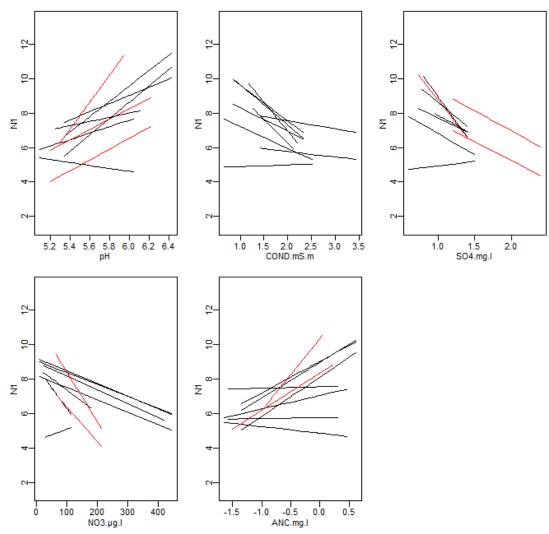


Figure 12. An example on the relationship (based on linear mixed effect models) between water chemistry and species diversity (N1exp) for rivers in Norway. Red lines denote significant trends (p < 0.05). See Table 4 and Table 5 for the relationship elsewhere.

Table 4. Number of sites with a significant correlation between species diversity $(N1_{exp})$ and measured water
chemistry variables in rivers. The correlations are either positive or negative in the table (positive/negative). n
denotes number of sites where both biological and chemical data are present, ANC denotes acid neutralizing
capacity and NA denotes that chemical data is not available.

RIVERS	n	рН	ANC	SO_4	NO_3	NH_4	Conductivity
Czech Republic	4	-	1/0	0/1	0/1	-	0/1
Germany	29	5/0	5/0	0/9	0/8	0/2	NA
Latvia	2	-	1/0	0/2	-	-	-
Norway	9	3/0	2/0	0/3	0/2	NA	-
Sweden	6	0/1	2/0	0/2	-	-	0/1
UK	11	1/0	-	-	-	NA	2/0
Total	61	9/1	11/0	0/17	0/11	0/2	2/2

Table 5. Number of sites with a significant correlation between species diversity $(N1_{exp})$ and measured water chemistry variables in lakes. The correlations are either positive or negative in the table (positive/negative). n denotes number of sites where both biological and chemical data are present, ANC denotes acid neutralizing capacity and NA denotes that chemical data is not available.

LAKES	n	рН	ANC	SO_4	NO_3	NH_4	Conductivity
Norway	20	0/1	0/1	1/0	1/3	NA	1/0
Sweden litt.	7	2/0	4/0	0/4	0/2	-	0/2
Sweden sublitt.	7	0/1	0/3	1/0	1/0	-	3/0
Sweden prof.	7	0/1	0/1	-	1/0	1/1	1/1
UK	6	1/0	-	1/1	-	NA	0/1
Total	47	1/3	4/5	3/5	3/5	1/1	5/4

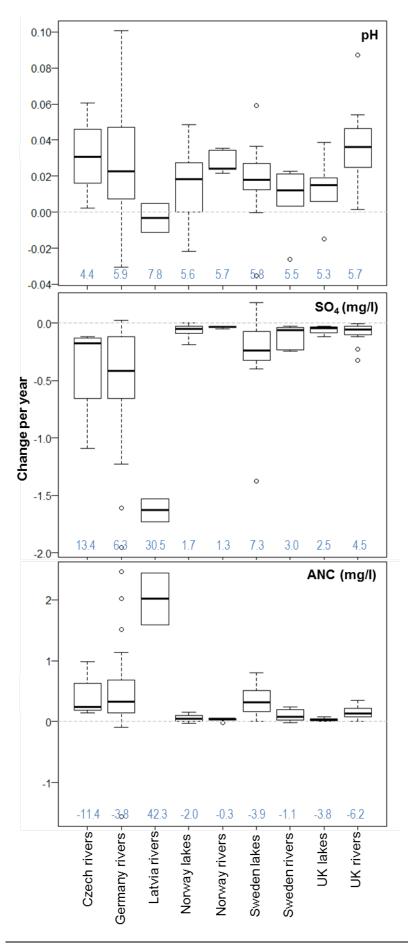


Figure 13. Boxplots showing change per year in pH, SO_4 and ANC during the water sampling periods covered by the different regions. Numbers along the base indicate the chemistry mean measurement for each country during the full sampling period. Note that measurements from the Swedish lake littoral-, sublittoral- and profundal samples indicated similar results and were lumped in the figure.

4. Discussion

4.1 Taxonomic resolution

In German rivers, Norwegian lakes and the sublittoral of Swedish lakes, taxonomic resolution increased steadily over the first years of the biological monitoring and then reached a plateau at which it has remained (Figures 5 and 6). This development is expected as the taxonomists steadily increased their skills. For the biological assemblages from the Norwegian rivers, Czech rivers, Swedish rivers and the UK lakes, the taxonomic resolution shows a pronounced U-shape with decreasing taxonomic resolution during the first years followed by an increasing trend towards the present. The decreasing resolution after the commencement of the sampling programmes is somewhat surprising. It may be that the decrease was caused by a monitoring focus on acid-sensitive indicator taxa and less focus on the full assemblage. After all, the programmes commenced in order to monitor the influence of acidification and not to capture the full biological communities. Then, as new biological acidification indices emerged (e.g., Moe et al., 2010), the list of acid-sensitive taxa expanded, leading to an increased taxonomic resolution.

By merging taxa and correcting for inconsistent taxonomic resolution, the data sensitivity may be coarser. However, without correction, the observed increase in α - diversity may partly or fully be attributed to the increased taxonomic resolution. For example, the diversity increase is statistically significant in the Norwegian lakes- and rivers prior to the taxonomic correction and not significant subsequent to the correction. Also, the diversity of the Swedish sublittoral was not significant prior to the correction and significant subsequent to the correction. The correction may explain possible discrepancies between our results and results from previous national studies.

The results highlight the importance of thoroughly testing for taxonomic consistency when studying long biological records from species data. Typically, multiple taxonomists have been involved over the years. The focus on biological groups may have changed according to the research question being asked at the time of sampling and according to taxonomic expertize. The skills of benthic invertebrate taxonomists are highly specialized and few can identify all groups. It is also clear that the taxonomic resolution may vary according to age of the specimen, since small stages are often hard to identify. Inevitably, some specimens in a sample cannot be identified reliably. Most larvae are typically small during summer and early autumn, but the larval size may also vary with food availability and temperature. Nevertheless, the fraction of unidentifiable larvae should be fairly stable over time and not influence the taxonomic consistency significantly, assuming there were no changes in seasonal sampling.

The altered taxonomic consistency also highlights the importance of performing internal standardization procedures and inter-calibration in biological inventories (e.g., Fjellheim et al., 2011). Biomonitoring is time-consuming and economically expensive. Society and research communities will

benefit if the data can be exploited fully, including for purpose other than those of the original exercise. At the same time, the value of the data depends on their quality.

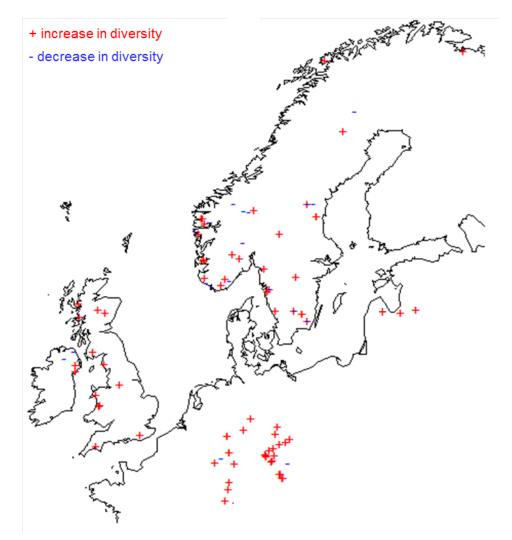


Figure 14. Trends in α - diversity (effective number of species, N1_{exp}) for zoobenthos in all rivers and lakes in the study. The linear trends are from a least squares model where + indicates an overall increase since the start of the site- specific sampling programme and – denotes a decrease. For the Norwegian rivers, note that not all trends are statistically significant (for significant trends, see Figures 8 and 9).

4.2 Temporal trends in species diversity (α- diversity)

A biological response to altered environmental conditions, such as the amelioration of acidification, will include at least one of three phenomena (modified from Guisan, 1995; Hengeveld, 1990): (1) unknown primary and secondary effects on the species and on the ecosystem, (2) biological migration such as a shift in ranges and (3) species extinction. Most, but not all sites, show an increased species diversity (Figure 14), even in a time of decreasing acidification and improved biological acidification indices. The recovery in terms of species diversity depends on the initial response to the acidification. For sites that were strongly acidified, e.g. in Germany and the Czech Republic, the recovery is expected to result in a significant increase in diversity. Such a recovery is seen for the German rivers

as a highly significant increase in species diversity. The diversity of three Czech rivers is increasing, albeit, not significantly since the diversity of Litavka River is decreasing. Litavka is the most acidified site of the Czech rivers (Horecký et al., 2006) and may a need as much as 50 years to recover (Hardekopf et al., 2008). The zoobenthos of Litavka is influenced by regular droughts during the summer (Horecký et al., 2013), however the decreasing diversity at this site (Figure 8) is most likely caused by the intensive forest clearings during the last two years of sampling. Notably, the forest clearing significantly influenced the water channel and damaged the river habitats and at the same time contributed to the both a chemical and a biological recovery in the stream (Stuchlík, personal observation), demonstrating the complexity of the recovery process. It is also important to consider that not all sites would be expected to show an increase in species diversity consequent upon chemical recovery. For example, the pre-disturbance community may have consisted of insensitive taxa, or the acidification eradicated fish populations (Hesthagen, 1986), allowing invertebrates that are sensitive to fish predation to flourish (Appelberg et al., 1993; Hildrew, 2009; Layer et al., 2011).

Interestingly, trends in the biota of the Swedish lakes depend on the habitat sampled. There has been a significant increase in the littoral, a significant decrease in the sublittoral, and no changes in the profundal. Environmental conditions in the shallow littoral fluctuate daily and/or seasonally, whereas the conditions are stable in the profundal. Such conditions include temperature, dissolved oxygen (DO), discharge from streams and abundance of macrophytes. All zones have experienced a similar recovery from acidification. However, the fauna of the profundal experiences more stable conditions and is less affected by the environmental changes that may accompany the recovery. DO may be a limiting factor in the profundal such that the influence from acidification is less pronounced.

When it comes to the divergent signals from the littoral sublittoral, it is interesting to note that the dissolved organic carbon (DOC) has increased significantly in these lakes during the last 25 years (data not shown, see also Monteith et al., 2007; Skjelkvåle et al., 1999). Such an increase in DOC has been observed in many regions and it has been suggested that the increase is linked to warmer conditions (Freeman et al., 2001) or to declining deposition of sulphur and sea salt (Monteith et al., 2007). DOC and water colour are generally correlated (Schindler et al., 1996; Wallage and Holden, 2010), suggesting that the depth of the photic zone, within which levels of light are sufficient to support the growth of aquatic macrophytes and algae, will become shallower. An increase in DOC may hence cause a declined autotrophic net primary production (Karlsson et al., 2009) and a reduction in the abundance and diversity of invertebrates as habitats and food types decrease. The relationship between light penetration and DOC is such that we would experience the biggest shifts in the photic zone in the sublittoral of boreal lakes. In addition, an increase in DOC could lead to a decline in DO and less favourable conditions for the fauna in the sublittoral. This is mainly because the chemocline will ascend and because the oxygen demand increases as the concentration of DOC increases (Wetzel, 2001). Similar processes may have occurred in the sublittoral elsewhere where the DOC has increased (Stendera and Johnson, 2008).

4.3 Relationship between environmental variables and species diversity

It is not straightforward to reach conclusions on the causes of the observed biodiversity increase. Worldwide, the biodiversity of freshwaters is declining (Sala et al., 2000). This decline is mostly caused by human impact, such as over-exploitation, water pollution, eutrophication, habitat degradation, species invasion and flow modification (Dudgeon et al., 2006). Such impacts may also lead to water shortages (Sala et al., 2005). These threats are unlikely to be acute at the sites we have studied, suggesting that other environmental variables have influenced the observed trends in species diversity. There are at least two environmental cues that potentially have changed in the study sites during the last 30 years; the deposition of long-range pollution has decreased (Monteith et al., 2007; Stoddard et al., 1999) and temperature has increased (EEA, 2012). Both can potentially influence biodiversity, either directly or indirectly.

According to our results, parts of the increased biodiversity can be attributed to a decrease in longrange pollution. This result emerges even from the spot- measurements of water chemistry in the study. The relationship would perhaps be more clear if continuous records of chemistry, or averages, were used. The relationship would clearly be more significant if the measurements were performed at the critical window of time over which the chemistry is influencing the biota. Many organisms cannot cope with low pH conditions (Raddum and Fjellheim, 1995; Raddum and Skjelkvale, 2001). When the pH lies outside the range tolerated by acid- sensitive taxa, they survive in refuges that are less influenced by acidification. As conditions improve, the sensitive taxa re-appear from the source populations. Such taxa form the basis for acidification indices and scores from these indices are now suggesting improved conditions in catchments from The Czech Republic, Germany, Norway, Sweden, UK and elsewhere (Angeler and Johnson, 2012; Hesthagen et al., 2011; Monteith et al., 2005; Murphy et al., in press).

In line with a decreased impact from long-range pollution, sulphate was the variable that was most significantly correlated with species diversity in the present study. The diversity at about one third of the riverine sites was significantly correlated with the concentration of sulphate. The concentration of sulphate in most sites in the present study varies from 1 to 20 mg/l, with the exceptions of two German rivers (Ettelsbach and Heidebach) and one Latvian river (Leila Jugla), with average concentrations above 165 mg/l and 40 mg/l, respectively. Sulphate is non-toxic at low concentrations, and its apparent importance in our analyses points to indirect effects on species diversity. It is not straightforward to separate collinear variables, such as pH, ANC, from the influence of sulphate. These variables are all associated with species diversity in the present study. Surrogate processes linked to sulphate may include the effects of a lowered pH that can influence the survival of aquatic insects directly, e.g., through the increase in hydrogen that interferes with the uptake and regulation of sodium and other ions (Havas and Rosseland, 1995; Paradise and Dunson, 1997), and indirectly, e.g., through aluminium toxicity (e.g., Havas and Rosseland, 1995; Sparling and Lowe, 1996).

There is increased species diversity at the Latvian sites. However, the chemistry of the Latvian rivers stands out compared to the other rivers in the study. The Latvian rivers have not experienced

acidification, and have high concentrations of copper, phosphorous and nitrogen. This suggests that the drivers of species diversity are different in Latvia compared to the other study sites. Either, the strong decreasing sulphate concentration has had a direct impact on biodiversity there, or the observed decrease in nitrogen-load has had a positive impact on the diversity.

We have not investigated the influence of temperature on species diversity. In order to do this, temperature means are needed for each site at the time of sampling, e.g., by using reanalysis approaches (http://www.ecmwf.int/research/era/do/get/index). This is an obvious next step, even though the air temperatures did not change significantly between 1990 and 2004 for many of the sites (supplementary information in Monteith et al., 2007). The influence of temperature change on species diversity is poorly understood and a simple correlation should not be expected (Walther et al., 2002). Factors affecting species distribution interact in complex ways and may influence any species directly or indirectly (Heller and Zavaleta, 2009; Mantyka-pringle et al., 2012). Species may disappear from parts of their original range and colonize new areas when the climate changes (Walther et al., 2002). In the case of rapid climate changes, not all species will be able to colonize new areas in sufficient time. Some studies report positive effects from climate change (e.g., Peterson et al., 2008), although, the general view is that climate change will cause major species extinctions (Bellard et al., 2012; Pereira et al., 2010; Thomas et al., 2004; Thuiller, 2007; Willis and Bhagwat, 2009).

4.4 Relationship between indices of species diversity and acidification

For some of the regions in the present study, such as Norway, the species diversity has not increased significantly in either lakes or rivers, despite a marked reappearance of sensitive taxa (Hesthagen et al., 2011; Moe et al., 2010; Raddum and Fjellheim, 1995) and despite a significant community response to temporal changes in water chemistry (Halvorsen et al., 2002; Halvorsen et al., 2003). When sensitive taxa re-appear, the acidification index will improve. The non-significant species diversity change at these sites suggests that a linear relationship between acidification indices and diversity indices should not be expected.

Acidification indices are based on the presence and abundance of acid-sensitive taxa in a sample, while species diversity indices are based on the presence and abundance of all taxa in a sample. At least three situations may induce shifts in acidification indices while the diversity indices remain more or less stable. (1) If the pre-disturbance community did not include sensitive taxa, then the acidification and the recovery did not necessarily lead to altered diversity. (2) In nature, the sensitive taxa and the tolerant taxa may interact by predation and competition causing unknown effects on diversity. For example, a sensitive species that re-appear and flourish may displace a tolerant species in the competition for space, food or other resources (Layer et al., 2010; Layer et al., 2013). (3) If acidification eradicated fish populations (Hesthagen, 1986), then the absence of a top-predator may disturb the community composition. Invertebrates that are sensitive to fish predation may flourish (Appelberg et al., 1993; Schofield et al., 1988), or sensitive taxa may survive in low pH-conditions since the total stress has no exceeded a critical limit for survival.

4.5 Sensitivity of species diversity in rivers versus lakes

The species diversity increase in the present study is more pronounced for rivers than for lakes. Also, the relationship between water chemistry and species diversity is equivocal for lakes and more distinct for rivers. These observations are somewhat counter-intuitive since rivers are more susceptible to temporal re-acidification events that may cause a lag in biological recovery (Ormerod and Durance, 2009). The re-acidification events occur during snow-melt in spring or during periods with heavy rain when pollutants are released during a short period. The water has not yet been buffered through soils causing a lower pH (Johannessen and Henriksen, 1978). In lakes, re-acidification events are rarer since potentially acidic water is diluted with resident water and ground water.

There are at least four non-exclusive theories that may explain the observations of a more pronounced species diversity response in rivers than in lakes. Three of these theories are founded on the homogeneity of lakes compared to rivers. E.g., rivers have highly fluctuating temperatures, fluctuating water chemistry, altered stream flow and channel instability (Lods-Crozet et al., 2001). (1) Because of the homogenous lake conditions, the original biodiversity of lakes was influenced by the acidification to a smaller extent than the biodiversity in the rivers. Hence, there is less potential for a diversity recovery in lakes. (2) The homogenous conditions in lakes may suggest a delayed chemical recovery so that the main chemical- and biological recovery have yet to occur. (3) The greater susceptibility of communities in streams to episodic shocks could make them more open to re-colonization compared to communities in lakes. In lakes, acid tolerant taxa dominate and these are more difficult to dislodge from their expanded niches. In other words, the community inertia is lower in rivers causing a faster response, including re-colonization. (4) Results from the streams may be more significant than results from the lakes because a larger fraction of the biota in streams is identified to species level. Abundant benthic macroinvertebrates in streams include mayflies (Ephemerptera), stoneflies (Plecoptera) and caddisflies (Trichoptera). The majority of these groups are identified to species level. In lakes, these insects are less abundant and non-biting midges (Chironomidae) form the most abundant benthic macroinvertebrate (Armitage et al., 1995). Non-biting midges are rarely identified below family-level for monitoring purpose, with the implication that the data resolution is lower in lakes than in streams. Supporting this, the most pronounced species diversity changes of lakes were found in Sweden with significant shifts both in α - diversity and β -diversity. Here, the data resolution is higher than in Norway and in the UK since the non-biting midges were identified to genus or species.

4.6 Assemblage changes over time (β-diversity)

The β -diversity of all assemblages has changed to some extent over time, e.g. as a response to recovery from acidification and addition of acid-sensitive taxa and/ or by natural drift. Overall, the assemblage changes differ among sites and inter-annual variability is masking any directional recovery in the species composition (Figure 11). This intern-annual variability may to some extend be random noise and/ or caused by differences in weather or sampling. Only the assemblages from the littoral zone of Swedish lakes show clear and directional changes in β -diversity. Either, the littoral of Swedish lakes has undergone unique environmental changes compared to the littoral of other regions, or a high

taxonomic resolution is needed to find a clear signal. The taxonomic resolution of the Swedish lakes is higher than the resolution from elsewhere and includes identification of the species-rich family of nonbiting midges. The taxonomic resolution is comparably high in the Swedish sublittoral and profundal samples. The sublittoral shows some directional changes in β -diversity, albeit less clear than the littoral signal, while there is no signal in the Swedish profundal. The lack of changes in the profundal could be caused by the homogenous conditions at greater depth compared to shallower areas. Our observations of directional change in the Swedish sites are supported by results from Johnson and Angeler (2010) who studied the littoral biological assemblages in several Swedish lakes, including three lakes from the present study. They concluded that the assemblage composition of acidified lakes has changes more than the assemblage composition in reference. They also found that the assemblages of acidified lakes now are becoming more similar to reference lakes. A varying degree of community responses is often found in acidified rivers in Northern Europe, even within single river system (Halvorsen et al., 2002; 2003; Sandlund et al., 2010). Nonlinear patterns of community change as a response to the chemical recovery have also been obtained from lakes in Canada (Lento et al., 2008). Together, this suggests that a biological recovery from acidification rarely will include clear directional or comparable changes among sites.

5. Implication of findings

5.1 Separating what is natural

Biological recovery from acidification includes a response to the reduced load of atmospheric pollutants, where the ideal end-point is the return to a natural or pre-acidified condition. Hence, conclusive results on the recovery can only be reached if comparable pre-state data are available. Unfortunately, information on the pre-state is lacking. A major focus for research on influence from acidification will be to separate what is natural and what is caused by man (e.g. Willis and Birks, 2006). Biological systems exhibit natural inter-annual variation that seemingly occurs under stable environmental conditions. Biological systems will also change as a response to environmental conditions. A response may be pronounced if thresholds, or so-called tipping points, are reached (Sonderegger et al., 2008). Tipping points can occur naturally when important ecotones are crossed or be induced by man.

Results from the current study suggest that there is no universally consistent pattern to biological recovery from acidification. A recovery in the community composition is likely to be site-specific. There is widespread evidence that acid-tolerant taxa have re-appeared, and concomitant increases in species diversity might therefore also be expected. It has, but not uniformly. There is a net increase in diversity, but for many sites, the increase is not statistically significant. For these sites, future records are needed to find whether the increase will be significant, or should be considered as natural non-significant variation. Also, more analyses are needed to separate the influence of a recovery from acidification from the influence of others stressors that have changed significantly during the last 25

years, such as temperature increase, DOC increase or eutrophication (e.g., Halvorsen et al., 2003; Stendera and Johnson, 2008).

5.2 Extrapolation of results

The present study includes a suite of lakes and rivers from six European countries. The sites were chosen as part of national monitoring programmes. Apart from acidification, the sites have limited human impact. Results from the study sites indicate some increase in species diversity during the last 20-30 years. Especially for many rivers, this increase is statistically significant. Results acquired for these sites should, with some precaution, be of general validity for similar sites and ecosystems. This suggests that a comparable increase in species diversity should be expected in acid-sensitive lakes and rivers elsewhere that show a chemical recovery and are otherwise little influenced by human activity. This is good news since the global biodiversity is at peril (UN, 2005). However, it is important to emphasize that the observed increase in species diversity should not be confused with a global increase in the total number of species. Most likely, the diversity has increased because species have immigrated from unacidified refugiae and/or because infrequent species have become more abundant. The study does not focus on single taxa and cannot conclude on new species, or whether threatened or rare species are now more abundant.

5.3 Ecosystem function

The link between biodiversity and ecosystem function is poorly understood. Many freshwater ecosystem functions are important for the services provided to society, such as the ecosystem ability to decompose organic matter, filter the water, break down toxic substances, or provide environments for recreational activities and fishing. For example, in a recent study Jenkins et al. (2013) found accelerated rates of decomposition in a headwater stream following long-term amelioration of acidity. Functions in an ecosystem are maintained by its members, the species, and the functional processes are mutually interdependent. A positive correlation has been found between species diversity and the number of functions that can be maintained within an ecosystem (Maestre et al., 2012), although the link between biodiversity and ecosystem processes are somewhat controversial. A significant decrease in diversity can be expected to cause a lowering of the ecosystems resilience (Elmqvist et al., 2003) and decreased rates of ecosystem processes (Dudgeon et al., 2006; Hooper et al., 2005). In other words, one function can be driven by more than one species in an ecosystem with high species diversity, suggesting that a loss of one species rarely influence the ecosystem. The implication is that an ecosystem with high species diversity is likely to have a better buffer capacity against pathogens or negative environmental impacts, such as pH decrease or rapid climate changes. The effect of diversity loss on ecosystem multifunctionality is particularly severe in harsh environments (Jucker and Coomes, 2012), implying that it is even more important to preserve biodiversity in harsh conditions. The species diversity of most sites in the present study is increasing. This gives hope for optimism considering that the ecosystems in the study now can be expected to have a higher buffer capacity against anticipated threats, such as climate change or habitat degradation.

5.4 Modelling

Given the global decline in biodiversity, ecosystem management would greatly benefit from accurate modelling of species diversity as a function of environmental scenarios or as a function of invasive species. Predictions of how biological communities may respond to future environments have so far largely been based on extrapolations from experimental and/or distributional studies on a few selected species in a restricted range of habitats (Jackson et al., 2009; Wilsey et al., 2013). In the present study, there are no clear directional changes in the biological communities (β -diversity) for the majority of the sites, even when most sites have undergone a similar chemical recovery from acidification. This suggests that it is not straightforward to model future assemblages of zoobenthos as a function of environmental scenarios. Future responses will likely be site-specific and non-directional, similar to the observed responses in the present study. These finding are also supported by paleolimnological records including sub-fossil benthic assemblages. The biological assemblages of most lakes will follow unique trajectories through time when affected by disturbance, unless crossing major ecotones, such as introduction or removal of macrophytes in the lake or vegetation in the catchment (Brodersen and Quinlan, 2006; Velle et al., 2005). That is, the variation among lakes remains larger than the variation within lakes.

When it comes to the modelling of α - diversity as a function of environmental variables, results from the present study are somewhat optimistic, and especially results from the rivers. The species diversity of rivers has responded to changes in water chemistry, such as sulphate, ANC and associated changes, suggesting that scenarios for water chemistry at these sites can successfully be used to model future species diversity. However, note that the relationship between water chemistry and species diversity is not evident for all sites and that a large fraction of the diversity changes are still unaccounted for. Previous studies on species diversity have reported varying degree of projected change (Pereira et al., 2010), implying large uncertainties in the model projections. Our results conform to this and also to findings by Stockdale et al. (in press) who found a good fit between model predictions and observations for biodiversity at some sites and poorer agreement for other sites. This suggests that careful site-specific model calibration is a prerequisite for successful modelling of α - diversity.

6. References

Angeler DG, Johnson RK (2012) Temporal scales and patterns of invertebrate biodiversity dynamics in boreal lakes recovering from acidification. Ecological Applications 22: 1172-1186.

Appelberg M, Henrikson BI, Henrikson L, Svedang M (1993) Biotic Interactions within the Littoral Community of Swedish Forest Lakes during Acidification. Ambio 22: 290-297.

Armitage PD, Cranston PS, Pinder LCV (1995) The Chironomidae: Biology and ecology of non-biting midges. London: Chapman & Hall.

Askew RR (1988) The dragonflies of Europe. Colchester: Harley Books.

Bady P, Dolédec S, Fesl C, Gayraud S, Bacchi M, Schöll F (2005) Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. Freshwater Biology 50: 159-173.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecology Letters 15: 365-377.

Birks HJB, Line JM (1992) The use of rarefaction analysis for estimating palynological richness from the quaternary pollen analytical data. The Holocene 2: 1-10.

Brodersen KP, Quinlan R (2006) Midges as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. Quaternary Science Reviews 25: 1995-2012.

Chapin Iii FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. Nature 405: 234-242.

Costanza R, Mageau M (1999) What is a healthy ecosystem? Aquatic Ecology 33: 105-115.

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guegan JF, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E, Turner JRG (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7: 1121-1134.

Dahl I, Hagebø E (2011) Intercomparison 1125: pH, Conductivity, Alkalinity, NO3-N, Cl, SO4, Ca, Mg, Na, K, TOC, Al, Fe, Mn, Cd, Pb, Cu, Ni, and Zn. Report no 107/2011. Oslo: NIVA, 75 pp.

DeBenedictis PA (1973) On the Correlations between Certain Diversity Indices. The American Naturalist 107: 295-302.

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Leveque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163-182.

EEA (2012) Climate change, impacts and vulnerability in Europe 2012. Copenhagen: European Environment Agency.

Elmqvist T, Folke C, Nystrom M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1: 488-494.

Evans CD, Cullen JM, Alewell C, Kopacek J, Marchetto A, Moldan F, Prechtel A, Rogora M, Vesely J, Wright R (2001) Recovery from acidification in European surface waters. Hydrology and Earth System Sciences 5: 283-297.

Fjellheim A, Johannessen A, Landås TS (2011) Biological intercalibration: Invertebrates 1511. ICP Waters report 109/2011. Oslo: NIVA.

Freeman C, Evans CD, Monteith DT, Reynolds B, Fenner N (2001) Export of organic carbon from peat soils. Nature 412: 785-785.

Frost S, Huni A, Kershaw WE (1971) Evaluation of a Kicking Technique for Sampling Stream Bottom Fauna. Canadian Journal of Zoology 49: 167-173.

Gleick PH (1996) Water resources. In Schneider, SH, editor, Encyclopedia of Climate and Weather, New York: Oxford University Press, 817–823.

Guisan A, editor(1995) Potential ecological impacts of climate change in the Alps and Fennoscandian mountains : an annex to the Intergovernmental Panel on Climate Change (IPCC) second assessment report, Working Group II-C (impacts of climate change on mountain regions). Genève: Conservatoire et jardin botaniques de la ville de Genève.

Halvorsen GA, Heegaard E, Raddum G (2002) Tracing recovery from acidification - a multivariate approach. ICP Waters report: NIVA, 39.

Halvorsen GA, Heegaard E, Fjellheim A, Raddum GG (2003) Tracing recovery from acidification in the western Norwegian Nausta watershed. Ambio 32: 235-239.

Hardekopf DW, Horecky J, Kopacek J, Stuchlik E (2008) Predicting long-term recovery of a strongly acidified stream using MAGIC and climate models (Litavka, Czech Republic). Hydrology and Earth System Sciences 12: 479-490.

Havas M, Rosseland BO (1995) Response of zooplankton, benthos, and fish to acidification: An overview. Water Air and Soil Pollution 85: 51-62.

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, Water, and Broad-Scale Geographic Patterns of Species Richness. Ecology 84: 3105-3117.

Hawksworth DJ (1995) Magnitude and distribution of biodiversity Global biodiversity Assessment.

Heino J (2005) Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. Freshwater Biology 50: 1578-1587.

Heino J (2008) Patterns of functional biodiversity and function-environment relationships in lake littoral macroinvertebrates. Limnology and Oceanography 53: 1446-1455.

Heino J (2009) Biodiversity of aquatic insects: spatial gradients and environmental correlates of assemblagelevel measures at large scales. Freshwater Reviews 2: 1-29.

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142: 14-32.

Hengeveld R (1990) Theories on species responses to variable climates. In Boer, M, de Groot, RS, editors, Landscape-ecological impact of climate change, Lunteren, The Netherlands, 274-293.

Hesthagen T (1986) Fish kills of Atlantic salmon (Salmo salar) and brown trout (Salmo trutta) in an acidified river of SW Norway. Water, Air, and Soil Pollution 30: 619-628.

Hesthagen T, Fjellheim A, Schartau AK, Wright RF, Saksgard R, Rosseland BO (2011) Chemical and biological recovery of Lake Saudlandsvatn, a formerly highly acidified lake in southernmost Norway, in response to decreased acid deposition. Sci Total Environ 409: 2908-2916.

Hildrew AG (2009) Sustained Research on Stream Communities: A Model System and The Comparative Approach. Advances in Ecological Research, Vol 41 41: 175-312.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75: 3-35.

Horecký J, Stuchlík E, Chvojka P, Bitušík P, Liška M, Pšenáková P, Špaček J (2002) Effects of acid atmospheric deposition on chemistry and benthic macroinvertebrates of forest streams in the Brdy Mts (Czech Republic). Acta Soc. Zool. Bohem. 66: 189-203.

Horecký J, Stuchlík E, Chvojka P, Hardekopf DW, Mihaljevic M, Špaček J (2006) Macroinvertebrate community and chemistry of the most atmospherically acidified streams in the Czech Republic. Water Air and Soil Pollution 173: 261-272.

Horecký J, Rucki J, Kram P, Krecek J, Bitušík P, Špaček J, Stuchlík E (2013) Differences in benthic macroinvertebrate structure of headwater streams with extreme hydrochemistry. Biologia 68: 303-313.

Huitfeldt-Kaas H (1922) On the cause of mass kill of salmon and brown trout in Frafjordelven, Helleelven and Dirdalselven, Ryfylke autumn 1920 (in Norwegian). Norsk Jæger og Fiskeforenings Tidsskrift 1: 37-44.

Hurlbert SH (1971) The Nonconcept of Species Diversity: A Critique and Alternative Parameters. Ecology 52: 577-586.

Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. Proceedings of the National Academy of Sciences of the United States of America 106: 19685-19692.

Jelks HL, Walsh SJ, Burkhead NM, Contreras-Balderas S, Diaz-Pardo E, Hendrickson DA, Lyons J, Mandrak NE, McCormick F, Nelson JS, Platania SP, Porter BA, Renaud CB, Schmitter-Soto JJ, Taylor EB, Warren ML (2008) Conservation Status of Imperiled North American Freshwater and Diadromous Fishes. Fisheries 33: 372-407.

Jenkins GB, Woodward G, Hildrew AG (2013) Long-term amelioration of acidity accelerates decomposition in headwater streams. Global Change Biology 19: 1100-1106.

Johannessen M, Henriksen A (1978) Chemistry of snow meltwater: Changes in concentration during melting. Water Resources Research 14: 615-619.

Johnson RK, Goedkoop W (2007) Bedömningsgrunder för bottenfauna i sjöar och vattendrag – Användarmanual och bakgrundsdokument. Uppsala: Swedish University of Agricultural Sciences, 84 pp.

Johnson RK, Angeler DG (2010) Tracing recovery under changing climate: response of phytoplankton and invertebrate assemblages to decreased acidification. Journal of the North American Benthological Society 29: 1472-1490.

Jost L (2006) Entropy and diversity. Oikos 113: 363-375.

Jucker T, Coomes DA (2012) Comment on "Plant Species Richness and Ecosystem Multifunctionality in Global Drylands". Science 337: 155.

Karlsson J, Bystrom P, Ask J, Ask P, Persson L, Jansson M (2009) Light limitation of nutrient-poor lake ecosystems. Nature 460: 506-U580.

Kernan M, Battarbee RW, Curtis CJ, Monteith DT, Shilland EM, editors(2010) Recovery of lakes and streams in the UK from the effects of acid rain. UK Acid Waters Monitoring Network 20 years Interpretative Report. London: Environmental Change Research Centre.

Lande R (1996) Statistics and Partitioning of Species Diversity, and Similarity among Multiple Communities. Oikos 76: 5-13.

Layer K, Riede JO, Hildrew AG, Woodward G (2010) Food Web Structure and Stability in 20 Streams Across a Wide pH Gradient. Advances in Ecological Research: Ecological Networks, Vol 42 42: 265-299.

Layer K, Hildrew AG, Jenkins GB, Riede JO, Rossiter SJ, Townsend CR, Woodward G (2011) Long-Term Dynamics of a Well-Characterised Food Web: Four Decades of Acidification and Recovery in the Broadstone Stream Model System. Advances in Ecological Research, Vol 44 44: 69-117.

Layer K, Hildrew AG, Woodward G (2013) Grazing and detritivory in 20 stream food webs across a broad pH gradient. Oecologia 171: 459-471.

Ledger ME, Hildrew AG (2005) The ecology of acidification and recovery: changes in herbivore-algal food web linkages across a stream pH gradient. Environmental Pollution 137: 103-118.

Lento J, Dillon PJ, Somers KM, Reid RA (2008) Changes in littoral benthic macroinvertebrate communities in relation to water chemistry in 17 Precambrian Shield lakes. Canadian Journal of Fisheries and Aquatic Sciences 65: 906-918.

Lento J, Dillon P, Somers K (2012) Evaluating long-term trends in littoral benthic macroinvertebrate communities of lakes recovering from acid deposition. Environmental Monitoring and Assessment 184: 7175-7187.

Lillehammer A (1988) Stoneflies (Plecoptera) of Fennoscandia and Denmark. København: E.J. Brill Scandinavian Science Press.

Lods-Crozet B, Lencioni V, Olafsson JS, Snook DL, Velle G, Brittain JE, Castella E, Rossaro B (2001) Chironomid (Diptera : Chironomidae) communities in six European glacier-fed streams. Freshwater Biology 46: 1791-1809.

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, Garcia-Gomez M, Bowker MA, Soliveres S, Escolar C, Garcia-Palacios P, Berdugo M, Valencia E, Gozalo B, Gallardo A, Aguilera L, Arredondo T, Blones J, Boeken B, Bran D, Conceicao AA, Cabrera O, Chaieb M, Derak M, Eldridge DJ, Espinosa CI, Florentino A, Gaitan J, Gatica MG, Ghiloufi W, Gomez-Gonzalez S, Gutierrez JR, Hernandez RM, Huang XW, Huber-Sannwald E, Jankju M, Miriti M, Monerris J, Mau RL, Morici E, Naseri K, Ospina A, Polo V, Prina A, Pucheta E, Ramirez-Collantes DA, Romao R, Tighe M, Torres-Diaz C, Val J, Veiga JP, Wang DL, Zaady E (2012) Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. Science 335: 214-218.

Mantyka-pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology 18: 1239-1252.

Mayhew PJ, Bell MA, Benton TG, McGowan AJ (2012) Biodiversity tracks temperature over time. Proceedings of the National Academy of Sciences of the United States of America 109: 15141-15145.

Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Moe SJ, Schartau AK, Baekken T, McFarland B (2010) Assessing macroinvertebrate metrics for classifying acidified rivers across northern Europe. Freshwater Biology 55: 1382-1404.

Monteith DT, Hildrew AG, Flower RJ, Raven PJ, Beaumont WRB, Collen P, Kreiser AM, Shilland EM, Winterbottom JH (2005) Biological responses to the chemical recovery of acidified fresh waters in the UK. Environmental Pollution 137: 83-101.

Monteith DT, Stoddard JL, Evans CD, de Wit HA, Forsius M, Hogasen T, Wilander A, Skjelkvale BL, Jeffries DS, Vuorenmaa J, Keller B, Kopacek J, Vesely J (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450: 537-U539.

Murphy JF, Winterbottom JH, Orton S, Simpson GL, Shilland EM, Hildrew AG (in press) Evidence of recovery from acidification in the macroinvertebrate assemblages of UK fresh waters: A 20-year time series. Ecological Indicators

Nilsson A (1996) Aquatic insects of North Europe : a taxonomic handbook. Stenstrup: Apollo Books.

Ormerod SJ, Durance I (2009) Restoration and recovery from acidification in upland Welsh streams over 25 years. Journal of Applied Ecology 46: 164-174.

Paradise CJ, Dunson WA (1997) Effects of pH and sulfate on insects and protozoans inhabiting treeholes. Archives of Environmental Contamination and Toxicology 33: 182-187.

Pereira HM, Leadley PW, Proenca V, Alkemade R, Scharlemann JPW, Fernandez-Manjarres JF, Araujo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guenette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496-1501.

Peterson AT, Stewart A, Mohamed KI, Araujo MB (2008) Shifting Global Invasive Potential of European Plants with Climate Change. PLoS ONE 3

Purvis A, Hector A (2000) Getting the measure of biodiversity. Nature 405: 212-219.

Raddum G (1993) Intercalibration of Invertebrate Fauna 9301. Bergen: Zoological Institute, University of Bergen, 26 pp.

Raddum GG, Hagenlund G, Halvorsen GA (1984) Effects of Lime Treatment on the Benthos of Lake Søndre Boksjø. Institute of Freshwater Research, Drottningholm Report No. 61: 167-176.

Raddum GG, Fjellheim A (1995) Acidification in Norway - Status and trends biological monitoring - Improvements in the invertebrate fauna. Water Air and Soil Pollution 85: 647-652.

Raddum GG, Skjelkvale BL (2001) Critical limit of acidifying compounds to invertebrates in different regions of Europe. Water Air and Soil Pollution 130: 825-830.

Rockstrom J, Steffen W, Noone K, Persson A, Chapin FS, Lambin EF, Lenton TM, Scheffer M, Folke C, Schellnhuber HJ, Nykvist B, de Wit CA, Hughes T, van der Leeuw S, Rodhe H, Sorlin S, Snyder PK, Costanza R, Svedin U, Falkenmark M, Karlberg L, Corell RW, Fabry VJ, Hansen J, Walker B, Liverman D, Richardson K, Crutzen P, Foley JA (2009) A safe operating space for humanity. Nature 461: 472-475.

Rohde K (1999) Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? Ecography 22: 593-613.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity - Global biodiversity scenarios for the year 2100. Science 287: 1770-1774.

Sala OE, Vuuren Dv, Pereira HM, Lodge D, Alder J, Cumming G, Dobson A, Wolters V, Xenopoulos MA, Zaitsev AS, Polo MG, Gomes Is, Queiroz C, Rusak JA (2005) Biodiversity across Scenarios. In Carpenter, S, Prabhu, L, Bennet, E, Zurek, M, editors, Ecosystems and Human Well-Being: Scenarios (Millennium Ecosystem Assessment Series) Washington, DC: Island Press, 375-408.

Sandlund OT, Bongard T, Brettum P, Finstad AG, Fjellheim A, Halvorsen GA, Halvorsen G, Hesthagen T, Hindar A, Papinska K, Saksgård R, Schartau AK, Schneider S, Skancke LB, Skjelbred B, Walseng B (2010)

Nettverk for biologisk mangfold i ferskvann – samlerapport 2010. NINA Rapport 598, Trondheim: Norsk institutt for naturforskning (NINA), 146 pp.

Schaumburg J, Maetze A, Lehmann R, Kifinger B, Coring E, Baltzer S (2008) Monitoringprogramm für versauerte Gewässer durch Luftschadstoffe in der Bundesrepublik Deutschland im Rahmen der ECE. Bericht der Jahre 2007-2008. Berlin: Bayerisches Landesamt für Umwelt, 134.

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413: 591-596.

Schindler DW (1988) Effects of acid-rain on fresh-water ecosystems. Science 239: 149-157.

Schindler DW, Curtis PJ, Parker BR, Stainton MP (1996) Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. Nature 379: 705-708.

Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. Ecological Monographs 80: 469-484.

Schofield K, Townsend CR, Hildrew AG (1988) Predation and the Prey Community of a Headwater Stream. Freshwater Biology 20: 85-95.

Skjelkvaale BL, de Wit HA (2011) Trends in precipitation chemistry, surface water chemistry and aquatic biota in acidified areas in Europe and North America from 1990 to 2008. ICP Waters Report 106/2011. Oslo.

Skjelkvåle BL, Mannio J, Wilander A, Andersen T (1999) Recovery from acidification of lakes in Finland, Norway and Sweden 1990–1999. Hydrology and Earth System Sciences 5: 327-338.

Smol JP, Wolfe AP, Birks HJB, Douglas MSV, Jones VJ, Korhola A, Pienitz R, Ruhland K, Sorvari S, Antoniades D, Brooks SJ, Fallu MA, Hughes M, Keatley BE, Laing TE, Michelutti N, Nazarova L, Nyman M, Paterson AM, Perren B, Quinlan R, Rautio M, Saulnier-Talbot E, Siitonen S, Solovieva N, Weckstrom J (2005) Climate-driven regime shifts in the biological communities of arctic lakes. Proceedings of the National Academy of Sciences of the United States of America 102: 4397-4402.

Solimini AG, Bazzanti M, Ruggiero A, Carchini G (2008) Developing a multimetric index of ecological integrity based on macroinvertebrates of mountain ponds in central Italy. Hydrobiologia 597: 109-123.

Sonderegger DL, Wang H, Clements WH, Noon BR (2008) Using SiZer to detect thresholds in ecological data. Frontiers in Ecology and the Environment 7: 190-195.

Sparling DW, Lowe TP (1996) Environmental hazards of aluminum to plants, invertebrates, fish, and wildlife. Rev Environ Contam Toxicol 145: 1-127.

Spyropoulou R, Martins IP, McInnes G, Uhel R, Uludag A, Herkendell J, Calvo EC, Romao C, Oulton AR, Weber J-L, Biala K, Lund MP, Makarewicz K, Hogeveen Y, Csagoly P, Petersen J-E, Schutyser F, Nieto A, Zisensis M, Richard D, McSharry B, Evans D (2010) The European environment. State and outlook 2010. Biodiversity. Luxembourg: Publications Office of the European Union.

Steffen W, Crutzen PJ, McNeill JR (2007) The Anthropocene: Are humans now overwhelming the great forces of nature. Ambio 36: 614-621.

Stendera S, Johnson RK (2008) Tracking recovery trends of boreal lakes: use of multiple indicators and habitats. Journal of the North American Benthological Society 27: 529-540.

Stendera S, Adrian R, Bonada N, Canedo-Arguelles M, Hugueny B, Januschke K, Pletterbauer F, Hering D (2012) Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. Hydrobiologia 696: 1-28.

Stockdale A, Tipping E, Fjellheim A, Garmo ØA, Hildrew AG, Lofts S, Monteith DT, Ormerod SJ, Shilland EM (in press) Recovery of macroinvertebrate species richness in acidified upland waters assessed with a field toxicity model. Ecological Indicators

Stoddard JL, Jeffries DS, Lukewille A, Clair TA, Dillon PJ, Driscoll CT, Forsius M, Johannessen M, Kahl JS, Kellogg JH, Kemp A, Mannio J, Monteith DT, Murdoch PS, Patrick S, Rebsdorf A, Skjelkvale BL, Stainton MP, Traaen T, van Dam H, Webster KE, Wieting J, Wilander A (1999) Regional trends in aquatic recovery from acidification in North America and Europe. Nature 401: 575-578.

Team RDC (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427: 145-148.

Thuiller W (2007) Biodiversity: Climate change and the ecologist. Nature 448: 550-552.

Tuomisto H (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33: 2-22.

UN (2005) The Millennium Ecosystem Assessment (MA), Ecosystems and Human Well-Being: Synthesis Island Press, Washington DC.

Velle G, Brooks SJ, Birks HJB, Willassen E (2005) Chironomids as a tool for inferring Holocene climate: an assessment based on six sites in southern Scandinavia. Quaternary Science Reviews 24: 1429-1462.

Walker SC, Poos MS, Jackson DA (2008) Functional rarefaction: estimating functional diversity from field data. Oikos 117: 286-296.

Wallace ID, Wallace B, Philipson GN (1990) A key to the case-bearing caddis larvae of Britain and Ireland. Ambleside: Freshwater Biological Association.

Wallage ZE, Holden J (2010) Spatial and temporal variability in the relationship between water colour and dissolved organic carbon in blanket peat pore waters. Sci Total Environ 408: 6235-6242.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416: 389-395.

Wathne BM, Ranneklev SB, Bjørn Olav Rosseland, Braaten HFV, Fjellheim A (2010) ICP Waters Programme Manual 2010. ICP Waters Report 105/2010.

Wetzel RG (2001) Limnology : lake and river ecosystems. San Diego: Academic Press.

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 280-338.

Willis KJ, Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation. Science 314: 1261-1265.

Willis KJ, Bhagwat SA (2009) Biodiversity and Climate Change. Science 326: 806-807.

Wilsey CB, Lawler JJ, Maurer EP, McKenzie D, Townsend PA, Gwozdz R, Freund JA, Hagmann K, Hutten KM (2013) Tools for Assessing Climate Impacts on Fish and Wildlife. Journal of Fish and Wildlife Management 4: 220-241.

Wright DH, Currie DJ, Maurer BA (1993) Species diversity in ecological communities: Historical and geographical perspectives In Ricklefs, RE, Schluter, D, editors, Energy supply and patterns of species richness on local and regional scales, Chicago University of Chicago Press, 66-76.

Appendix A. Study sites

Details on the rivers included in the analyses. WGS84 North and East indicate the geographical position given as decimal degrees, the dates indicate the time interval of the biological sampling, while the biological and the chemical samples indicate the total number of samples. St. = sampling station. The Swedish lakes include separate samples from the littoral (lit.), the sublittoral (sublit.) and the profundal (prof.)

Rivers

Country	River name	WGS84 North	WGS84 East	Altitude (m)	Date from	Date to	Biological samples	Chemica samples
Czech	Certovo lake - inflow	49.166667	13.196390	1027	09.07.1999	12.10.2011	13	13
Republic	Cerné lake - inflow	49.176390	13.181390	1008	09.07.1999	12.10.2011	9	9
	Litavka-krmelec	49.657560	13.868901	700	27.01.1999	14.10.2011	23	23
	Lysina	50.033868	12.666550	850	20.06.2000	04.08.2010	13	13
Germany	Dürreychbach	48.750167	8.443167	878	09.04.1987	18.11.2009	29	29
	Eger	50.085000	11.824500	691	11.09.1989	21.04.2009	29	29
	Elberndorfer Bach	50.987833	8.201333	573	25.07.1988	09.11.2009	46	46
	Ettelsbach	51.117333	12.757500	196	07.05.1992	20.10.2005	52	52
	Goldersbach	47.874167	8.055167	1061	01.05.1986	19.11.2009	33	33
	Große Ohe	49.924000	7.619167	544	21.10.1982	17.03.2003	15	15
	Große Pyra	50.409667	12.533500	805	02.06.1992	24.10.2009	57	57
	Gräfenbach	48.934667	13.408500	813	09.06.1983	26.06.2008	24	24
	Heidebach Hinterer	51.425833	12.923333	160	01.10.1992	25.10.2006	42	42
	Schachtenbach	48.938500	13.408500	818	09.06.1983	24.06.2008	23	23
	Kleine Kinzig	48.419833	8.358833	725	15.09.1985	01.11.2007	29	29
	Lange Bramke	51.855000	10.421000	609	17.04.1986	13.11.2009	37	37
	Nieste 3	51.287333	9.737167	446	05.08.1987	07.04.2004	46	46
	Rombach 2	50.041167	11.900833	732	31.07.1989	21.04.2009	29	29
	Rombach 3	50.206333	8.436167	581	30.07.1987	14.04.2004	59	59
	Rote Pockau	50.204833	8.436167	571	30.07.1987	21.10.1997	47	47
	Röslau	50.617167	13.191167	667	29.07.1992	17.08.2009	58	58
	Schmerbach 1	49.655333	8.887000	366	05.07.1987	18.04.2000	20	20
	Schmerbach 3	48.939667	13.405333	840	10.02.1983	24.06.2008	20	20
	Seebach	50.835000	14.125000	409	17.09.1992	09.10.2006	53	53
	Taubenbach	49.718667	7.109833	632	10.06.1983	02.04.2008	18	18
	Traunbach Vorderer	48.935833	13.408500	824	10.02.1983	26.06.2008	23	23
	Schachtenbach	49.769167	12.421333	745	29.05.1985	14.04.2010	52	52
	Waldnaab 2	49.789000	12.424167	661	16.07.1984	15.04.2010	52	52
	Waldnaab 8	50.722000	13.706167	796	23.03.1992	04.08.2009	67	67
	Wilde Weißeritz	50.319000	12.136833	578	24.03.1992	25.05.2009	30	30
	Wolfsbach	51.001167	8.203333	576	25.07.1988	09.11.2009	48	48

Country	River name	WGS84 North	WGS84 East	Altitude (m)	Date from	Date to	Biological samples	Chemica samples
	Zinnbach	50.005333	11.900833	715	20.03.1989	04.05.2009	28	28
	Zinse	50.205556	8.433056	715	18.04.2000	14.04.2004	8	8
Latvia	Tulja	57.136100	25.903599	177	01.03.1997	03.10.2011	19	19
	Amula	57.014052	22.646257	38	01.10.1997	05.10.2011	8	0
	Liela Jugla	56.971429	24.487392	12.5	01.03.1997	26.10.2011	19	19
Norway	Gaular st1	61.342580	6.454540	734	20.05.1989	26.10.2010	42	0
	Gaular st2	61.335860	6.358440	514	20.05.1989	26.10.2010	44	0
	Gaular st3	61.345530	6.321230	454	20.05.1989	26.10.2010	44	0
	Gaular st4	61.319450	6.232740	315	20.05.1989	26.10.2010	44	30
	Gaular st5	61.339724	6.130927	179	20.05.1989	26.10.2010	44	30
	Gaular st6	61.420080	6.438230	359	20.05.1989	26.10.2010	44	0
	Gaular st7	61.420030	6.376580	308	20.05.1989	26.10.2010	44	0
	Gaular st8	61.415130	6.346640	298	20.05.1989	26.10.2010	44	0
	Gaular st9	61.409810	6.279640	297	20.05.1989	26.10.2010	44	0
	Gaular st10	61.366020	6.232480	296	20.05.1989	26.10.2010	43	0
	Gaular st11	61.360870	6.148880	167	20.05.1989	26.10.2010	44	0
	Gaular st12	61.353980	6.121600	206	20.05.1989	26.10.2010	44	0
	Gaular st13	61.326990	5.805500	70	20.05.1989	26.10.2010	44	0
	Gaular st14	61.313520	5.794800	122	20.05.1989	27.10.2010	44	0
	Gaular st15	61.338780	5.727760	61	20.05.1989	27.10.2010	44	0
	Gaular st16	61.362420	5.722830	27	20.05.1989	27.10.2010	44	0
	Gaular st17	61.368700	5.685540	14	20.05.1989	27.10.2010	44	0
	Nausta st1	61.605410	6.004760	416	22.05.1989	29.10.2009	34	0
	Nausta st2	61.600330	5.988230	340	22.05.1989	29.10.2009	34	0
	Nausta st3	61.583420	5.970680	297	22.05.1989	29.10.2009	34	0
	Nausta st4	61.583110	5.967040	296	22.05.1989	27.09.2001	26	0
	Nausta st5	61.583660	5.945930	280	22.05.1989	27.09.2001	26	0
	Nausta st6	61.578170	5.941180	254	22.05.1989	29.10.2009	34	0
	Nausta st7	61.577850	5.940560	256	22.05.1989	29.10.2009	34	28
	Nausta st8	61.574660	5.902470	231	22.05.1989	29.10.2009	34	0
	Nausta st9	61.576930	5.895030	222	22.05.1989	29.10.2009	34	28
	Nausta st10	61.576410	5.841400	117	22.05.1989	29.10.2009	34	0
	Nausta st11	61.576790	5.829890	98	22.05.1989	29.10.2009	34	28
	Nausta st12	61.569114	5.790368	59	22.05.1989	29.10.2009	33	27
	Nausta st13	61.567650	5.781560	50	22.05.1989	29.10.2009	34	0
	Nausta st14	61.558150	5.786350	38	22.05.1989	27.09.2001	26	0
	Nausta st15	61.551680	5.789450	41	22.05.1989	27.09.2001	26	0
	Nausta st16	61.544700	5.785710	35	22.05.1989	29.10.2009	34	0
	Nausta st17	61.540210	5.783980	29	22.05.1989	29.10.2009	34	0
	Nausta st18	61.538800	5.749430	62	22.05.1989	29.10.2009	34	0
	Nausta st19	61.524860	5.739690	25	22.05.1989	27.09.2001	26	0
	Nausta st20	61.516760	5.719830	39	22.05.1989	29.10.2009	34	0
	Vikedal st1	59.595915	6.115150	498	27.05.1987	01.11.2010	48	0

Country	River name	WGS84 North	WGS84 East	Altitude (m)	Date from	Date to	Biological samples	Chemical samples
	Vikedal st2	59.591009	6.115147	445	27.05.1987	01.11.2010	48	0
	Vikedal st3	59.592190	6.113746	463	27.05.1987	01.11.2010	48	0
	Vikedal st4	59.570721	6.051634	169	27.05.1987	01.11.2010	48	0
	Vikedal st5	59.570263	6.051754	172	27.05.1987	01.11.2010	48	0
	Vikedal st6	59.571235	6.047376	163	27.05.1987	01.11.2010	48	0
	Vikedal st7	59.564351	6.013394	217	26.05.1987	01.11.2010	48	0
	Vikedal st8	59.564570	6.027323	157	26.05.1987	01.11.2010	48	0
	Vikedal st9	59.557096	5.997110	173	26.05.1987	01.11.2010	48	0
	Vikedal st10	59.554102	5.996860	163	26.05.1987	01.11.2010	48	44
	Vikedal st11	59.545902	5.997740	164	26.05.1987	20.10.2010	48	43
	Vikedal st12	59.544102	6.000860	169	26.05.1987	01.11.2010	48	26
	Vikedal st13	59.535837	5.971723	73	27.05.1987	01.11.2010	37	0
	Vikedal st14	59.536504	6.000680	271	27.05.1987	19.11.2010	36	0
	Vikedal st15	59.518067	5.949904	65	27.05.1987	19.11.2010	36	0
	Vikedal st16	59.515128	5.930665	64	27.05.1987	19.11.2010	36	0
	Vikedal st17	59.516461	5.929642	56	27.05.1987	22.10.2010	48	0
	Vikedal st18	59.498621	5.911628	14	27.05.1987	19.11.2010	36	0
	Vikedal st19	59.541517	5.976415	132	14.05.1998	01.11.2010	24	0
	Vikedal st20	59.523051	5.964823	66	14.05.1998	19.11.2010	14	0
	Vikedal st21	59.520701	5.943405	64	14.05.1998	01.11.2010	14	0
	Vikedal st22	59.519801	5.935652	63	14.05.1998	01.11.2010	14	0
Sweden	Laxtjärnsbäcken	65.785696	19.087667	442	08.09.1986	18.09.2011	13	13
	Lill-Fämtan	60.843351	13.122309	465	31.10.1985	26.10.2011	17	17
	Lommabäcken Nedre	58.703493	14.637273	160	05.11.1985	18.10.2011	17	17
	Muddusälven	66.765754	20.124686	165	29.09.2000	11.09.2011	12	12
	Pipbäcken Nedre	57.066475	12.792359	97	16.10.1986	03.10.2011	16	16
	Stormyrbäcken	62.260475	16.272243	414	05.06.1987	18.10.2011	16	16
UK	Afon Gwy	57.117775	-3.849592	325	12.04.1988	07.05.2010	23	22
	Afon Hafren	56.758386	-5.612152	10	11.04.1988	05.05.2010	23	22
	Allt a Mharcaidh	55.070701	-4.399182	260	08.04.1988	04.05.2010	22	21
	Allt na Coire nan Con	53.486530	-1.814450	280	09.05.1988	28.04.2010	23	21
	Beaghs Burn	50.505040	-4.020739	225	24.04.1988	13.04.2007	19	15
	Bencrom River	51.045507	0.075663	94	25.04.1988	06.04.2010	23	22
	Coneyglen Burn	52.474051	-3.703369	380	05.05.1988	17.04.2010	22	21
	Dargall Lane	52.453855	-3.732024	380	04.05.1991	17.04.2010	19	18
	Narrator Brook Old Lodge (Ashdown	55.086709	-6.174419	150	14.04.1988	12.04.2007	20	18
	Sands)	54.157310	-6.005030	140	15.04.1988	06.05.2009	22	20
	River Etherow	54.739432	-7.004671	230	13.04.1989	10.04.2007	18	16

Lakes

Country	Lake name	WGS84 North	WGS84 East	Altitu de (m)	L.area (km²)	Date from	Date to	Biologic samples	Chem. sample
Norway	Atnsjøen	61.885171	10.144376	701	4.80	01.04.1998	01.10.2010	26	26
	Bjorvatn	58.518766	8.448941	226	0.28	01.04.1997	01.10.2010	28	26
	Bredtjenn	59.113412	11.678199	190	0.26	01.04.1997	01.10.2010	28	13
	Dalvatn	69.697924	30.357462	132	0.35	01.04.1997	01.10.2010	28	13
	Heddersvatn	59.831720	8.736000	1136	1.83	01.04.1997	01.10.2010	28	15
	Kapervatn	58.604380	8.039731	503	0.07	01.04.1997	01.10.2010	28	13
	Langtjern	69.248909	17.415713	168	1.32	01.04.1997	01.10.2010	28	8
	Lille Hovvatn	60.366034	9.730607	518	0.23	01.04.1997	01.10.2010	28	14
	Ljosvatn	58.415959	6.211179	150	0.19	01.04.1997	01.10.2010	28	26
	Lomstjørni	58.676381	6.081700	242	0.07	01.04.1997	01.10.2010	28	19
	Markusdalsv.	60.895060	5.255795	96	1.43	01.04.1997	01.10.2010	28	26
	Nystølvatn	61.344976	6.487335	715	1.25	01.04.1997	01.10.2010	28	24
	Røyravatn	59.605410	9.467070	450	0.11	01.04.1997	01.10.2010	28	28
	Rondvatn	61.896423	9.799177	1167	1.03	01.04.1997	01.10.2010	28	14
	Saudlandsvatn	59.544043	6.024644	230	0.42	01.04.1997	01.10.2010	28	24
	Sognevatn	58.203981	6.764016	110	0.14	01.04.1997	01.10.2010	28	25
	Stortjørna	58.316398	7.675419	268	0.27	01.04.1997	01.10.2010	28	14
	Svartdalsvatn	61.983599	10.758875	868	0.28	01.04.1997	01.10.2010	28	8
	Svartetjern	60.835200	5.572140	302	0.06	01.04.1997	01.10.2010	28	21
	Øvre Jerpetjern	62.278357	8.842000	1018	0.64	01.04.1997	01.10.2010	28	21
Sweden	Brunnsjön lit.	56.597200	15.728070	100	0.10	30.10.1986	25.10.2010	27	27
	Brunnsjön prof. Brunnsjön	56.597200	15.728070	100	0.10	30.10.1986	25.10.2010	34	33
	sublit	56.597200	15.728070	100	0.10	24.04.1991	25.10.2010	24	24
	Fiolen lit.	57.080435	14.532324	227	1.55	28.04.1988	18.10.2010	26	26
	Fiolen prof.	57.080435	14.532324	227	1.55	28.04.1988	18.10.2010	33	33
	Fiolen sublit.	57.080435	14.532324	227	1.55	19.04.1989	18.10.2010	27	27
	Fräcksjön lit.	58.151381	12.179369	60	0.26	06.11.1986	05.11.2010	27	27
	Fräcksjön prof	58.151381	12.179369	60	0.26	06.11.1986	05.11.2010	34	33
	Fräcksjön sublit	58.151381	12.179369	60	0.26	19.04.1989	05.11.2010	28	28
	Härsvatten lit. Härsvatten	58.020200	12.030390	137	0.18	29.04.1988	13.10.2010	25	25
	prof. Härsvatten	58.020200	12.030390	137	0.18	29.04.1988	13.10.2010	33	33
	sublit	58.020200	12.030390	137	0.18	12.04.1989	13.10.2010	27	27
	Stensjön lit.	61.643253	16.585637	268	0.53	23.10.1986	15.10.2009	26	26
	Stensjön profun	61.643253	16.585637	268	0.53	23.10.1986	11.10.2010	34	33
	Stensjön sublit	61.643253	16.585637	268	0.53	23.05.1989	11.10.2010	28	28
	Storasjö lit.	56.944310	15.276425	252	0.35	28.10.1986	20.10.2010	26	26
	Storasjö profun	56.944310	15.276425	252	0.35	28.10.1986	20.10.2010	31	17
	Storasjö sublit	56.944310	15.276425	252	0.35	10.04.1991	02.10.1995	7	7
	Tväringen lit.	62.241186	15.694044	308	1.61	10.08.1988	13.10.2010	22	22
	Tväringen	62.241186	15.694044	308	1.61	10.08.1988	15.10.2010	29	13

Country	Lake name	WGS84 North	WGS84 East	Altitu de (m)	L.area (km ²)	Date from	Date to	Biologic samples	Chem. samples
	profun				(
	Tväringen sublit	62.241186	15.694044	308	1.61	17.05.1989	15.10.2010	14	14
UK	Coire nan Arr	57.417136	-5.651864	125	0.12	11.04.1988	08.05.2007	20	20
	Lochnagar Round Loch of	56.958266	-3.231570	785	0.10	13.04.1988	08.05.2010	23	23
	Glenhead	55.093738	-4.430448	295	0.13	08.04.1988	04.05.2010	22	22
	Scoat Tarn	54.481952	-3.299546	602	0.05	07.04.1988	08.04.2010	22	22
	Llyn Llagi	53.014902	-4.015300	380	0.06	22.04.1988	17.04.2010	23	23
	Blue Lough	54.427931	-5.955019	340	0.02	13.04.1989	06.05.2009	22	20

Appendix B. – Taxonomic consistency

Taxa with inconsistent taxonomy through time. These were merged to the coarsest taxonomic unit. Some additional taxa were merged because of misspellings or inconsistent nomenclature (taxa not shown here).

Norway lakes

- Diura nanseni + Diura sp.
- Halesus radiatus + Halesus sp.
- Leptophlebia marginata + Leptophlebia sp + Leptoplebia vespertina
- Limnephilidae ind + Limnephilus centralis + Limnephilus marmoratus + Limnephilus rhombicus + Limnephilus sp + Limnephilus sparsus
- Nemoura avicularis + Nemoura cinerea + Nemoura sp
- Siphlonurus aestivalis + Siphlonurus alternatus + Siphlonurus lacustris + Siphlonurus sp

Sweden lakes

- Micronecta sp. + Micronecta poweri.
- Stictochironomus sp. + Stictochironomus rosenschoeldi
- Dicrotendipes sp. + D.modestus
- Polypedilum sp. + Polypedilum laetum gr. + Polypedilum breviantennatum gr.
- Tanypodinaae sp. + Ablabesmyia longistyla + Ablabesmyia monilis + Ablabesmyia phatta + Ablabesmyia sp.+ Conchapelopia sp + Krenopelopia sp. + Macropelopia sp. + Paramerina sp. + Pentaneurini + Procladius sp. + Thienemannimyia
- Theromyzon sp. + Theromyzon tessulatum
- Tubifex tubifex + Tub. without h.setae + Tub. with h.setae + Naididae+Limnodrilus
- Chaoborus sp. + Chaoborus obscuripes + Chaoborus flavicans + Chaoborus crystallinus
- Lephtophlebia sp. + Leptophlebia vespertina+ Leptophlebia marginata

UK lakes

- Mystacides azurea + Mystacides sp.
- Capnia atra + Capnia sp.
- Plectrocnemia conspersa + Plectrocnemia sp.
- Tipula sp. + TIPULIDAE
- Paraleptophelia (misspelled!) + LEPTOPHLEBIIDAE
- Athripsodes aterrimus + Athripsodes sp.
- Cyrnus flavidus + Cyrnus sp. + Cyrnus trimaculatus
- Halesus radiates + Halesus sp.
- Polycentropus flavomaculatus + Polycentropus sp.
- Limnephilidae sp. + Limnephilidae. sp.

German rivers

- Agapetus + Agapetus fuscipes + Agapetus nimbulus
- Amphinemura + Amphinemura borealis + Amphinemura standfussi + Amphinemura sulcicollis
- Chironomidae + Chironomini + Chironomus sp. + Corynoneura + Diamesa + Heterotrissocladius + Macropelopia + Orthocladiinae + Prodiamesa olivacea + Rheotanytarsus + Tanypodinae + Tanytarsini sp. + Pseudodiamesa branickii
- Brachyptera + Brachyptera risi + Brachyptera seticornis + Brachyptera starmachi
- Capnia + Capnia nigra + Capnia vidua
- Lumbriculidae + Lumbriculus variegatus + Stylodrilus heringianus + Tubifex + Tubificidae + Nais
 + Naididae + Limnodrilus
- Plectrocnemia + Plectrocnemia conspersa + Plectrocnemia geniculate
- Siphonoperla + Siphonoperla torrentium
- Simuliidae + Simulium + Simulium (Boophthora) erythrocephalum + Simulium (Eusimulium) angustipes + Simulium (Eusimulium) aureum + Simulium (Nevermannia) brevidens + Simulium (Nevermannia) carpathicum + Simulium (Nevermannia) cryophilum + Simulium (Nevermannia) latigonium + Simulium (Nevermannia) lundstromi + Simulium (Nevermannia) natural + Simulium (Nevermannia) urbanum + Simulium (Nevermannia) vernum + Simulium (Wilhelmia) equinum + Simulium argyreatum + Simulium monticola + Simulium noelleri + Simulium ornatum + Simulium reptans + Simulium trifasciatum + Simulium tuberosum + Simulium variegatum Gruppe
- Protonemura + Protonemura auberti + Protonemura austriaca + Protonemura intricate + Protonemura lateralis + Protonemura meyeri + Protonemura Montana + Protonemura nimborum + Protonemura nitida + Protonemura praecox

Latvia

- Baetis niger + Baetis rhodani + Baetis
- Atherix ibis + Atherix sp.
- Halesus digitatus + Halesus interpunctata + Halesus radiates + Halesus sp.

Norway rivers

 Agabus sp. + Agapetus sp. + Coleoptera indet. + Berosus sp. + Deronectes latus + Dytiscidae indet. + Elmidae indet. + Elmis aenea + Elodes sp. + Haliplus sp. + Helophorus sp. + Hydraena sp. + Hydraena gracilis + Hydroporus sp. + Limnius volckmari + Nebrioporus assimilis + Nebrioporus depressus + Oulimnius tuberculatus + Platambus maculatus + Stictotarsus multilineatus

Czech Republic

- Simuliidae sp. + Simulium sp. + Simulium cf. cryophilum

Sweden rivers

No changes

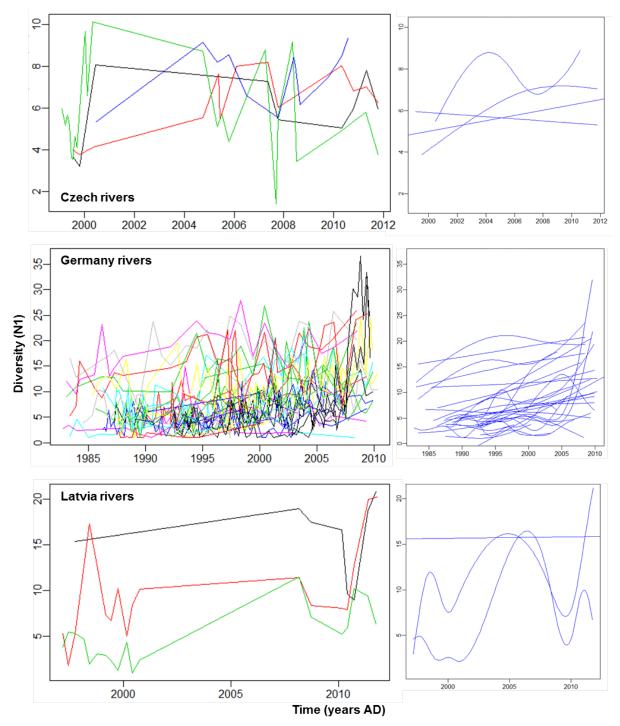
UK rivers

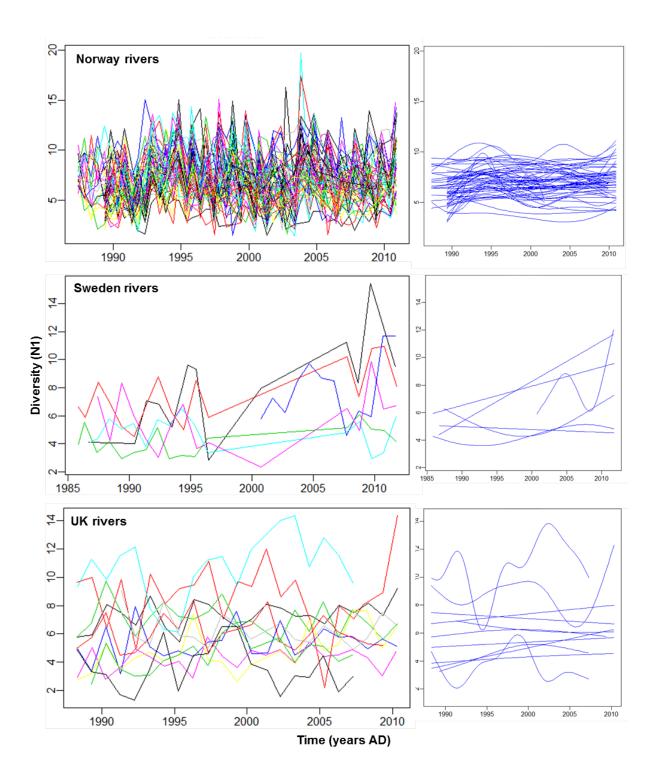
No changes

Appendix C. – Diversity details

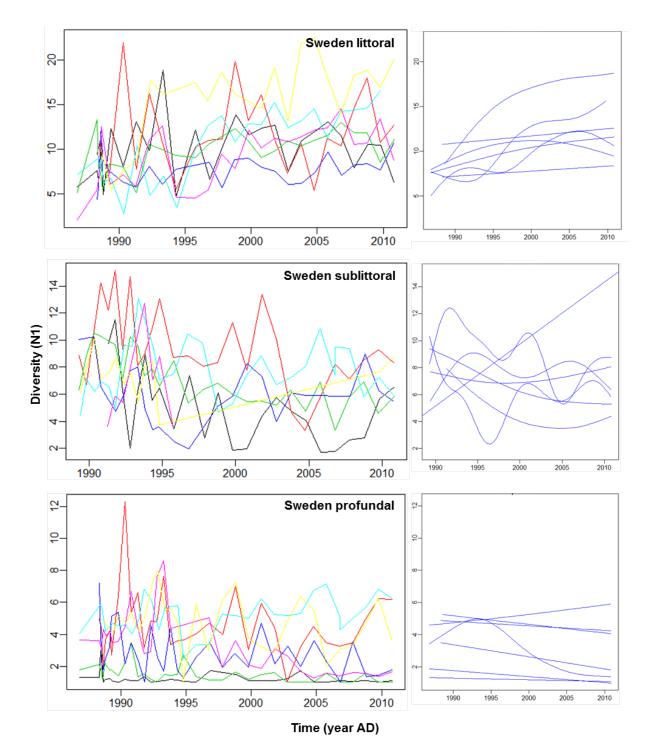
The figures below give some details on the biodiversity (effective number of species, N1) of rivers and lakes included in the analyses. Figures in left column show raw biodiversity and figures on the right display GAM fitted to the biodiversity data. Lowermost figure shows β -diversity analysed by non-metric multidimensional scaling (NMDS) in countries missing from Figure 11. The trajectories (lines) show assemblage changes from the 1980s and towards the present. Closely placed samples have a similar species composition.

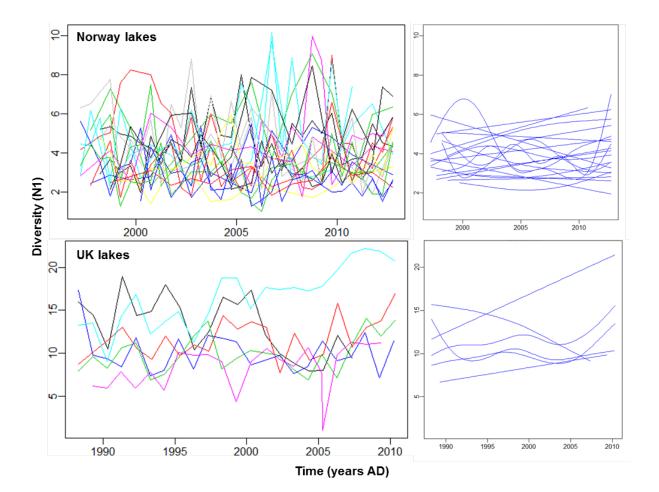
a-diversity of rivers

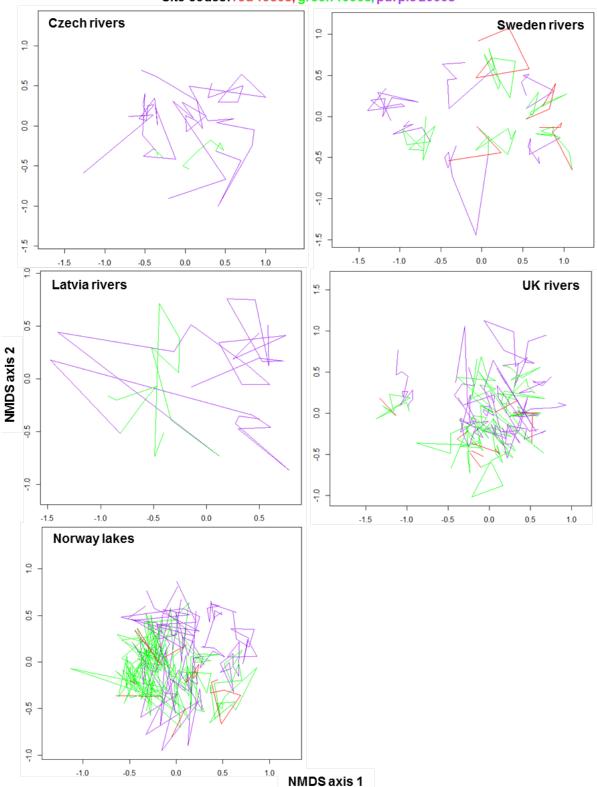




a-diversity of lakes







β -diversity of the sites that are not shown in main text

Site codes: red 1980s, green 1990s, purple 2000s

Appendix D. Reports and publications from ICP Waters

All reports from the ICP Waters programme from 2000 up to present are listed below. Reports before year 2000 can be listed on request. All reports are available from the Programme Centre. Reports and recent publications are also accessible through the ICP Waters website; http://www.icp-waters.no/

- Escuedero-Oñate, C. Intercomparison 1327: pH, Conductivity, Alkalinity, NO3-N, Cl, SO4, Ca, Mg, Na, K, TOC, Al, Fe, Mn, Cd, Pb, Cu, Ni and Zn. ICP Waters Report 116/2013
- Holen, S., R.F. Wright, I. Seifert. 2013. Effects of long-range transported air pollution (LTRAP) on freshwater ecosystem services. ICP Waters Report 115/2013
- Velle, G., Telford, R.J., Curtis, C., Eriksson, L., Fjellheim, A., Frolova, M., Fölster J., Grudule N., Halvorsen G.A., Hildrew A., Hoffmann A., Indriksone I., Kamasová L., Kopáček J., Orton S., Krám P., Monteith D.T., Senoo T., Shilland E.M., Stuchlík E., Wiklund M.L., de Wit, H., Skjelkvaale B.L. 2013. Biodiversity in freshwaters. Temporal trends and response to water chemistry. ICP Waters Report 114/2013
- Fjellheim, A., Johannessen, A. and Landås, T.S. 2013. Biological intercalibration: Invertebrates 1612. ICP Waters Report 113/2013
- Skjelkvåle, B.L., Wathne, B.M., de Wit, H. and Michela Rogora (eds.) 2013. Proceedings of the 28th Task Force meeting of the ICP Waters Programme in Verbania Pallanza, Italy, October 8 10, 2012. **ICP Waters Report 112/2013**
- Dahl, I. 2012. Intercomparison 1226: pH, Conductivity, Alkalinity, NO3-N, Cl, SO4, Ca, Mg, Na, K, TOC, Al, Fe, Mn, Cd, Pb, Cu, Ni and Zn. ICP Waters report 111/2012
- Skjelkvåle, B.L., Wathne B. M. and Moiseenko, T. (eds.) 2010. Proceedings of the 27th meeting of the ICP Waters Programme Task Force in Sochi, Russia, October 19 – 21, 2011. **ICP Waters report 110/2012**
- Fjellheim, A., Johannessen, A., Svanevik Landås, T. 2011. Biological intercalibration: Invertebrates 1511. NIVA-report SNO 6264-2011, ICP Waters report 109/2011.
- Wright, R.F., Helliwell, R., Hruska, J., Larssen, T., Rogora, M., Rzychoń, D., Skjelkvåle, B.L. and Worsztynowicz, A. 2011. Impacts of Air Pollution on Freshwater Acidification under Future Emission Reduction Scenarios; ICP Waters contribution to WGE report. NIVA-report SNO 6243-2011. ICP Waters report 108/2011.
- Dahl, I and Hagebø, E. 2011. Intercomparison 1125: pH, Cond, HCO3, NO3-N, Cl, SO4, Ca, Mg, Na, K, TOC, Al, Fe, Mn, Cd, Pb, Cu, Ni, and Zn. NIVA-report SNO 6222-2011. **ICP Waters report 107/2011.**
- Skjelkvåle B.L. and de Wit, H. (Eds). 2011. Trends in precipitation chemistry, surface water chemistry and aquatic biota in acidified areas in Europe and North America from 1990 to 2008. NIVA-report SNO 6218-2011 ICP Waters report 106/2011.
- ICP Waters Programme Centre 2010. ICP Waters Programme manual. NIVA SNO 6074-2010. ICP Waters report 105/2010. 91 s. ISBN 978-82-577-5953-7,
- Skjelkvåle, B.L., Wathne B. M. and Vuorenmaa J. (eds.) 2010. Proceedings of the 26th meeting of the ICP Waters Programme Task Force in Helsinki, Finland, October 4 – 6, 2010. **ICP Waters report 104/2010**
- Fjellheim, A. 2010. Biological intercalibration: Invertebrates 1410. NIVA-report SNO 6087-2010, ICP Waters report 103/2010.
- Hovind, H. 2010. Intercomparison 1024: pH, Cond, HCO₃, NO₃-N, Cl, SO₄, Ca, Mg, Na, K, TOC, Al, Fe, Mn, Cd, Pb, Cu, Ni, and Zn. NIVA-report SNO 6029-2010. **ICP Waters report 102/2010.**
- De Wit, H. A. and Lindholm M., 2010. Nutrient enrichment effects of atmospheric N deposition on biology in oligotrophic surface waters a review. NIVA-report SNO 6007 2010. ICP Waters report 101/2010
- Skjelkvåle, B.L., De Wit, H and and Jeffries, D. (eds.) 2010. Proceedings of presentations of national activities to the 25th meeting of the ICP Waters Programme Task Force in Burlington, Canada, October 19-21 2009. NIVA-report SNO 5995 2010. ICP Waters report 100/2010.
- Fjellheim, A. 2009. Biological intercalibration: Invertebrates 1309. NIVA-report SNO 5883-2009, ICP Waters report 99/2009.
- Hovind, H. 2009. Intercomparison 0923: pH, Cond, HCO₃, NO₃-N, Cl, SO₄, Ca, Mg, Na, K, TOC, Al, Fe, Mn, Cd, Pb, Cu, Ni, and Zn. NIVA-report SNO 5845-2009. **ICP Waters report 98/2009**.

- Ranneklev, S.B., De Wit, H., Jenssen, M. T. S. and Skjelkvåle, B.L., 2009. An assessment of Hg in the freshwater aquatic environment related to long-range transported air pollution in Europe and North America. NIVA-report SNO 5844-2009. **ICP Waters report 97/2009.**
- Skjelkvåle, B.L., Jenssen, M. T. S. and De Wit, H (eds.) 2009. Proceedings of the 24th meeting of the ICP Waters Programme Task Force in Budapest, Hungary, October 6 – 8, 2008. NIVA-report SNO 5770-2009. ICP Waters report 96/2008.
- Fjellheim, A and Raddum, G.G. 2008. Biological intercalibration: Invertebrates 1208. NIVA-report SNO 5706-2008, ICP Waters report 95/2008
- Skjelkvåle, B.L., and De Wit, H. (eds.) 2008. ICP Waters 20 year with monitoring effects of long-range transboundary air pollution on surface waters in Europe and North-America. NIVA-report SNO 5684-2008. ICP Waters report 94/2008.
- Hovind, H. 2008. Intercomparison 0822: pH, Cond, HCO₃, NO₃-N, Cl, SO₄, Ca, Mg, Na, K, Fe, Mn, Cd, Pb, Cu, Ni, and Zn. NIVA-report SNO 5660-2008. **ICP Waters report 93/2008**.
- De Wit, H. Jenssen, M. T. S. and Skjelkvåle, B.L. (eds.) 2008. Proceedings of the 23rd meeting of the ICP Waters Programme Task Force in Nancy, France, October 8 10, 2007. NIVA-report SNO 5567-2008. **ICP Waters report 92/2008.**
- Fjellheim, A and Raddum, G.G. 2008. Biological intercalibration: Invertebrates 1107. NIVA-report SNO 5551 2008, ICP Waters report 91/2008
- Hovind, H. 2007. Intercomparison 0721: pH, Cond, HCO3, NO3-N, Cl, SO4, Ca, Mg, Na, K, Fe, Mn, Cd, Pb, Cu, Ni, and Zn. NIVA-report SNO 5486-2007. **ICP Waters report 90/2007**
- Wright, R.F., Posch, M., Cosby, B. J., Forsius, M., and Skjelkvåle, B. L. 2007. Review of the Gothenburg Protocol: Chemical and biological responses in surface waters and soils. NIVA-report SNO 5475-2007. ICP Waters report 89/2007
- Skjelkvåle, B.L., Forsius, M., Wright, R.F., de Wit, H., Raddum, G.G., and Sjøeng, A.S.M. 2006. Joint Workshop on Confounding Factors in Recovery from Acid Deposition in Surface Waters, 9-10 October 2006, Bergen, Norway; Summary and Abstracts. NIVA-report SNO 5310-2006. ICP Waters report 88/2006.
- De Wit, H. and Skjelkvåle, B.L. (eds). 2007. Trends in surface water chemistry and biota; The importance of confounding factors. NIVA-report SNO 5385-2007. ICP Waters report 87/2007.
- Hovind, H. 2006. Intercomparison 0620. pH, K25, HCO3, NO₃ + NO₂, Cl, SO₄, Ca, Mg, Na, K, total aluminium, aluminium reactive and nonlabile, TOC, COD-Mn. Fe, Mn, Cd, Pb, Cu, Ni and Zn. NIVA-report SNO 5285-2006. **ICP Waters** report 86/2006.
- Raddum, G.G. and Fjellheim, A. 2006. Biological intercalibration 1006: Invertebrate fauna. NIVA-report SNO 5314-2006, ICP Waters report 85/2006.
- De Wit, H. and Skjelkvåle, B.L. (eds.) 2006. Proceedings of the 21th meeting of the ICP Waters Programme Task Force in Tallinn, Estonia, October 17-19, 2005. NIVA-report SNO 5204-2006, **ICP Waters report 84/2006.**
- Wright, R.F., Cosby, B.J., Høgåsen, T., Larssen, T., Posch, M. 2005. Critical Loads, Target Load Functions and Dynamic Modelling for Surface Waters and ICP Waters Sites. NIVA-report SNO 5166-2005. ICP Waters report 83/2006.
- Hovind, H. 2005. Intercomparison 0317. pH, K25, HCO3, NO3 + NO2, Cl, SO4, Ca, Mg, Na, K, total aluminium, aluminium reactive and nonlabile, TOC, COD-Mn. Fe, Mn, Cd, Pb, Cu, Ni and Zn. NIVA-report SNO 5068-2005. **ICP Waters** report 82/2005
- Raddum, G.G. 2005. Intercalibration 0307: Invertebrate fauna. NIVA-report SNO 5067-2005. ICP Waters report 81/2005
- De Wit, H. and Skjelkvåle, B.L (eds.). 2005. Proceedings of the 20th meeting of the ICP Waters Programme Task Force in Falun, Sweden, October 18-20, 2004. NIVA-report SNO 5018-2005, **ICP Waters report 80/2005**.
- Fjeld, E., Le Gall, A.-C. and Skjelkvåle, B.L. 2005. An assessment of POPs related to long-range air pollution in the aquatic environment. NIVA-report SNO 5107-2005, **ICP Waters report 79/2005.**
- Skjelkvåle et al 2005. Regional scale evidence for improvements in surface water chemistry 1990-2001. *Environmental Pollution, 137: 165-176*
- Hovind, H. 2004. Intercomparison 0418. pH, K25, HCO3, NO3 + NO2, Cl, SO4, Ca, Mg, Na, K, Fe, Mn, Cd, Pb, Cu, Ni and Zn. NIVA-report SNO 4875-2004, **ICP Waters report 78/2004.**
- Raddum, G.G. 2004. Intercalibration: Invertebrate fauna 09/04. NIVA-report SNO 4863-2004, ICP Waters report 77/2004.
- Skjelkvåle, B.L. (ed). Proceedings of the 19th meeting of the ICP Waters Programme Task Force in Lugano, Switzerland, October 18-20, 2003. NIVA-report SNO 4858-2004, **ICP Waters report 76/2004.**
- Raddum, G.G, *et al.* 2004. Recovery from acidification of invertebrate fauna in ICP Water sites in Europe and North America. NIVA-report SNO 4864-2004, **ICP Waters report 75/2004.**
- Hovind, 2003. Intercomparison 0317. pH, K25, HCO3, NO3 + NO2, Cl, SO4, Ca, Mg, Na, K, total aluminium, aluminium reactive and nonlabile, TOC, COD-Mn. Fe, Mn, Cd, Pb, Cu, Ni and Zn. NIVA-report SNO 4715-2003, ICP Waters report 74/2003.

Skjelkvåle, B.L. (ed). 2003. The 15-year report: Assessment and monitoring of surface waters in Europe and North America; acidification and recovery, dynamic modelling and heavy metals. NIVA-report SNO 4716-2003, **ICP Waters report** 73/2003.

Raddum.G.G. 2003. Intercalibration 0307: Invertebrate fauna. NIVA-report SNO-4659-2003, ICP Waters report 72/2003.

- Skjelkvåle, B.L. (ed.). 2003. Proceedings of the 18th meeting of the ICP Waters Programme Task Force in Moscow, October 7-9, 2002. NIVA-report SNO 4658-2003, **ICP Waters report 71/2002**.
- Wright, R.F and Lie, M.C. 2002.Workshop on models for Biological Recovery from Acidification in a Changing Climate. 9-11 september 2002 in Grimstad, Norway. Workshop report. NIVA-report 4589-2002.
- Jenkins, A. Larssen, Th., Moldan, F., Posch, M. and Wrigth R.F. 2002. Dynamic Modelling of Surface Waters: Impact of emission reduction - possibilities and limitations. NIVA-report SNO 4598-2002, ICP Waters report 70/2002.
- Halvorsen, G.A, Heergaard, E. and Raddum, G.G. 2002. Tracing recovery from acidification a multivariate approach. NIVA-report SNO 4564-2002, ICP Waters report 69/2002.
- Hovind. H. 2002. Intercomparison 0216. pH, K₂₅, HCO₃, NO₃ + NO₂, Cl, SO₄, Ca, Mg, Na, K, total aluminium, aluminium reactive and nonlabile, TOC, COD-Mn. Fe, Mn, Cd, Pb, Cu, Ni and Zn. NIVA-Report SNO 4558-2002, ICP Waters Report 68/2002.
- Skjelkvåle, B.L. and Ulstein, M. (eds). 2002. Proceedings from the Workshop on Heavy Metals (Pb, Cd and Hg) in Surface Waters; Monitoring and Biological Impact. March 18-20, 2002, Lillehammer, Norway. NIVA-report SNO-4563-2002, ICP Waters report 67/2002.
- Raddum.G.G. 2002. Intercalibration 0206: Invertebrate fauna. NIVA-report SNO-4494-2002, ICP Waters report 66/2002.
- Bull, K.R. Achermann, B., Bashkin, V., Chrast, R. Fenech, G., Forsius, M., Gregor H.-D., Guardans, R., Haussmann, T., Hayes, F., Hettelingh, J.-P., Johannessen, T., Kryzanowski, M., Kucera, V., Kvaeven, B., Lorenz, M., Lundin, L., Mills, G., Posch, M., Skjelkvåle, B.L. and Ulstein, M.J. 2001. Coordinated Effects Monitoring and Modelling for Developing and Supporting International Air Pollution Control Agreements. *Water Air Soil Poll.* 130:119-130.
- Hovind, H. 2001. pH, K₂₅, HCO₃, NO₃ + NO₂, Cl, SO₄, Ca, Mg, Na, K, total aluminium, aluminium reactive and nonlabile, TOC, COD-Mn. Fe, Mn, Cd, Pb, Cu, Ni and Zn. NIVA-Report SNO 4416-2002, **ICP Waters report 64/2001**.
- Lyulko, I. Berg, P. and Skjelkvåle, B.L. (eds.) 2001. National presentations from the 16th meeting of the ICP Waters Programme task Force in Riga, Latvia, October 18-20, 2000. NIVA-report SNO 4411-2001. **ICP Waters report 63/001**.
- Raddum.G.G. 2000. Intercalibration 0005: Invertebrate fauna. NIVA-report SNO4384-2001, ICP Waters report 62/2001.
- Raddum, G.G. and Skjekvåle B.L. 2000. Critical Load of Acidifying Compounds to Invertebrates In Different Ecoregions of Europe. *Water Air Soil Poll.* **130**:825-830.
- Stoddard, J. Traaen, T and Skjelkvåle, B.L. 2001. Assessment of Nitrogen leaching at ICP-Waters sites (Europe and North America). *Water Air Soil Poll*. **130**:825-830.
- Skjelkvåle, B.L. Stoddard J.L. and Andersen, T. 2001. Trends in surface waters acidification in Europe and North America (1989-1998). *Water Air Soil Poll*.**130**:781-786.
- Kvaeven, B. Ulstein, M.J., Skjelkvåle, B.L., Raddum, G.G. and Hovind. H. 2001. ICP Waters An international programme for surface water monitoring. *Water Air Soil Poll*.**130**:775-780.
- Wright, R.F. 2001. Note on: Effect of year-to-year variations in climate on trends in acidification. NIVA-report SNO 4328-2001, ICP Waters report 57/2001.
- Hovind, H. 2000. Trends in intercomparisons 8701-9812: pH, K₂₅, NO₃ + NO₂, Cl, SO₄, Ca, Mg, Na, K and aluminium reactive and nonlabile, TOC, COD-Mn. NIVA-Report SNO 4281-2000, **ICP Waters Report 56/2000**.
- Hovind, H. 2000. Intercomparison 0014. pH, K₂₅, HCO₃, NO₃ + NO₂, Cl, SO₄, Ca, Mg, Na, K, total aluminium, aluminium reactive and nonlabile, TOC, COD-Mn. Fe, Mn, Cd, Pb, Cu, Ni and Zn. NIVA-Report SNO 4281-2000, ICP Waters Report 55/2000.
- Skjelkvåle, B.L., Olendrzynski, K., Stoddard, J., Traaen, T.S, Tarrason, L., Tørseth, K., Windjusveen, S. and Wright, R.F. 2001. Assessment of trends and leaching in Nitrogen at ICP Waters Sites (Europe And North America). NIVA-report SNO 4383-2001, ICP Waters report 54/2001.
- Stoddard, J. L., Jeffries, D. S., Lükewille, A., Clair, T. A., Dillon, P. J., Driscoll, C. T., Forsius, M., Johannessen, M., Kahl, J. S., Kellogg, J. H., Kemp, A., Mannio, J., Monteith, D., Murdoch, P. S., Patrick, S., Rebsdorf, A., Skjelkvåle, B. L., Stainton, M. P., Traaen, T. S., van Dam, H., Webster, K. E., Wieting, J., and Wilander, A. 1999. Regional trends in aquatic recovery from acidification in North America and Europe 1980-95. Nature 401:575- 578.
- Skjelkvåle, B. L., Andersen, T., Halvorsen, G. A., Raddum, G.G., Heegaard, E., Stoddard, J. L., and Wright, R. F. 2000. The 12-year report; Acidification of Surface Water in Europe and North America; Trends, biological recovery and heavy metals. NIVA-Report SNO 4208/2000, ICP Waters report 52/2000.

Reports before year 2000 can be listed on request.

NIVA: Norway's leading centre of competence in aquatic environments

NIVA provides government, business and the public with a basis for preferred water management through its contracted research, reports and development work. A characteristic of NIVA is its broad scope of professional disciplines and extensive contact network in Norway and abroad. Our solid professionalism, interdisciplinary working methods and holistic approach are key elements that make us an excellent advisor for government and society.





Gaustadalléen 21 • NO-0349 Oslo, Norway Telephone: +47 22 18 51 00 • Fax: 22 18 52 00 www.niva.no • post@niva.no